Poultry Breeding

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MORLEY A. JULL

UNIVERSITY OF MARYLAND

Third Edition

JOHN WILEY & SONS, INC. · NEW YORK
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1 · Breeds and Varieties
of Chickens

From time immemorial, chickens have entered closely into human life in a variety of ways

Chickens were originally, and still are, of chief interest to mankind because of their eggs, which have a very high nutritional value   In the early days of the development of the poultry industry in most countries, chicken meat was of secondary importance, since game birds were often relatively abundant   Feathers, first used for ornamental decoration, found use in pillows and mattresses and in numerous other ways   The domestication of the ancestors of modern breeds was brought about largely as a result of their economic importance in providing food for human beings

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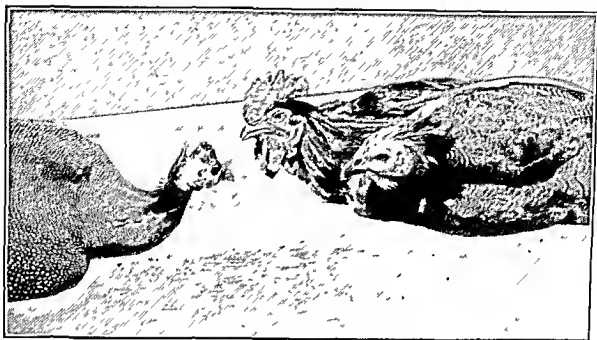
Fig. 1. Left to right, guinea female, Rhode Island Red male, and the progeny of these birds. (E. M. Funk, 1938.)

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Fig. 2. Left, a chicken-turkey hybrid removed dead from the shell on the twenty-eighth day of incubation: it was secured from a mating of a Rhode Island Red male × Bronze turkey female. (Quinn, Burrows, and Byerly, U. S. Dept. Agr.) Right, the hybrid progeny secured from a pheasant male × chicken bantam female cross.

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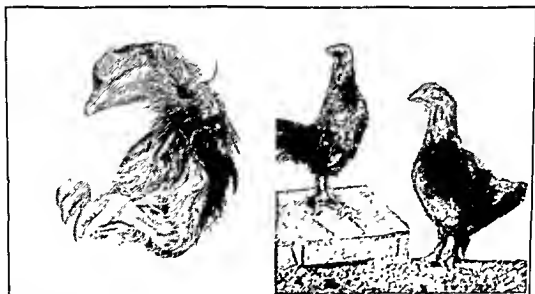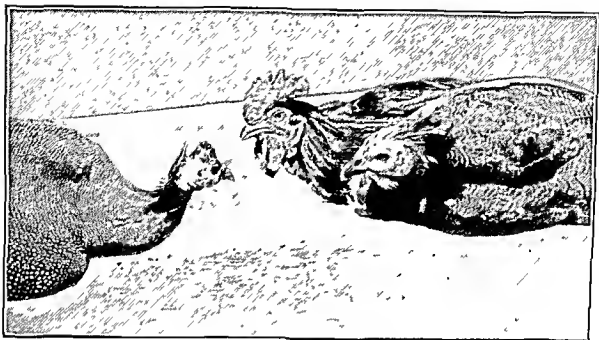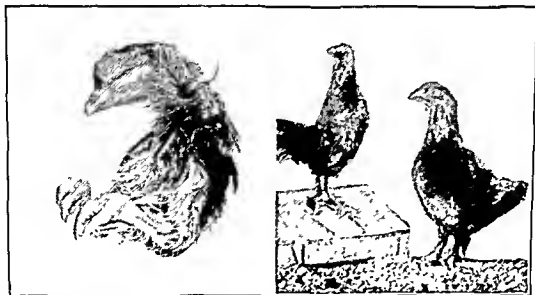

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All four wild species will cross with one another, and the hybrids are more or less fertile among themselves Also, from evidence supplied by naturalists and investigators who have made crosses between each of the four wild species and domestic stocks, it appears that all hybrid progeny are fertile with the possible exception of the female offspring of the cross between the *Gallus varius* male and domestic females Apparently most of the modern-day breeds are descended from these four wild species (Houwink 1921, Ghigi 1922 and 1934, and Lotsy and Kuiper 1924)

The plumage pattern of the Red Junglefowl male closely resembles that of the modern Black-Breasted Red Game male and to a considerable extent that of the modern Brown Leghorn male The plumage pattern of the Red Junglefowl female resembles that of the modern Black-Breasted Game Bantam female and to a slightly less degree that of the Light Brown Leghorn female Beebe (1918–1922), in his detailed description of fourteen Red Junglefowl skins of males in the collection of the American Museum of Natural History, observed that there were varying shades of buff, brown, and red in different specimens Among seven skins of females in the same collection, Beebe also observed variations in shade of plumage coloration in certain sections Darwin (1890) stated that the plumage pattern of *Gallus gallus* varied considerably

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of its sickle and saddle feathers, which attain a length from about 6 to 20 feet

Belgian breeds of poultry have been developed primarily for food production The Campine, which derived its name from the Campine district of Belgium, where it was bred most extensively, is of interest to poultry geneticists because it is a "hen-feathered" breed, by which is meant that the male hackle, sickle, and saddle feathers are of the same shape as comparable feathers in the female The Braekel was derived from and resembles the Campine The Malines is one of the largest of the Belgian breeds and is an excellent meat-producing breed

British breeds and varieties are quite numerous and vary a great deal in size, shape, and other characters Since mention has already been made of the widespread interest in cockfighting in Great Britain since early times, it is natural to expect that game breeds were popular Several varieties and strains of English Games were developed Among the most popular utility British breeds are the Dorking, Orpington, and Sussex, all of which have white skin The Dorking is one of the few breeds that have a red earlobe but lay a white shelled egg, and it has five toes The Cornish Game, now known as the Cornish, was originally produced in Cornwall and for many years was bred in England principally for exhibition, according to Brown (1929) Spangled and Black Hamburgs, with pointed spikes projecting upwards from their rose combs, were evolved in Britain The Scotch Gray, with barred plumage, is another red-earlobe, white-egg breed

Dutch breeds include the Barnvelder, which lays a very dark-brown shelled egg, the Breda, a white earlobe breed, and the White-Crested Black Dutch, apparently descended from the White-Crested Black Polish, the white crest never having been observed in the wild species

French poultry breeders developed numerous breeds, much attention having been paid to the meat-producing qualities of certain breeds Among the more important French breeds are the Crevecoeur, the Houdan, the Faverolle, and the La Fleche The peculiar feature of the Crevecoeur is its divided comb with the two points well apart The Houdan is a five-toed breed with a crest, muffs, and a beard, none of which was present in the four wild species The La Fleche also has a horned comb

Among the German breeds of poultry, only the Creeper and the Lakenfelder need be mentioned Both of these breeds are illustrated in later sections of this book and need not be described further here

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by feather contour In some cases comb type is a breed characteristic, for example, all Plymouth Rocks, Delawares, and New Hampshires have single combs whereas all Wyandottes have rose combs Leghorns, Anconas, and Minorcas have white earlobes whereas New Hampshires, Plymouth Rocks, and Rhode Island Reds have red earlobes For the most part, the standard weight of the cock, hen, cockerel, and pullet is a breed characteristic

Varieties within a Breed. Within each of several breeds of chickens in which there have been developed two or more varieties, the distinguishing characteristic is plumage color or pattern and sometimes shape of comb For instance, the Leghorn breed contains the following varieties White, Buff, Black, Black-Tailed Red, Columbian, Dark Brown, Light Brown, Red, and Silver The Plymouth Rock breed contains the following varieties Barred, Buff, White, Columbian, Partridge, and Silver-Penciled

In the Rhode Island Red breed, there are the single-comb and rose-comb varieties, comb shape being the distinguishing characteristic between the two varieties Some of the Leghorn varieties are subdivided into single-comb and rose-comb subvarieties

Plumage Colors and Patterns. From the standpoint of plumage color, the breeds and varieties may be divided into two groups (1) breeds and varieties that are of one color and are called self-colored or solid-colored, (2) breeds and varieties with plumage of two or more colors The self-colored group includes the whites, blacks, and blues

Among the parti-colored breeds and varieties there is a great array of color patterns involving two or more colors within each feather covering certain parts of the body Feathers with black and white bars are encountered in the Barred Plymouth Rock, Silver Campine and Silver-Penciled Hamburg (see Fig 4) It may be noted here that there are also Golden Campines and Golden-Penciled Hamburgs in which the white in the Silver Campine and Silver-Penciled Hamburg is replaced with "gold" color Other black-and-white markings within the feather occur in the Silver-Spangled Hamburg, Ancona, and Speckled Sussex (see Fig 5) There is also a Golden-Spangled Hamburg

Lacing and penciling of feathers are two outstanding characteristics that determine plumage pattern in several varieties Penciled feathers are present in Dark Cornish, Partridge Cochins, and Silver-Penciled Wyandottes In Partridge Wyandottes, the white of the Silver-Penciled variety is replaced with gold Lacing is found in the Silver-Laced Wyandotte (the Golden-Laced variety being the counterpart) Blue Andalusian, and the White-Laced Red Cornish Different laced and penciled varieties are shown in Figs 6 and 7

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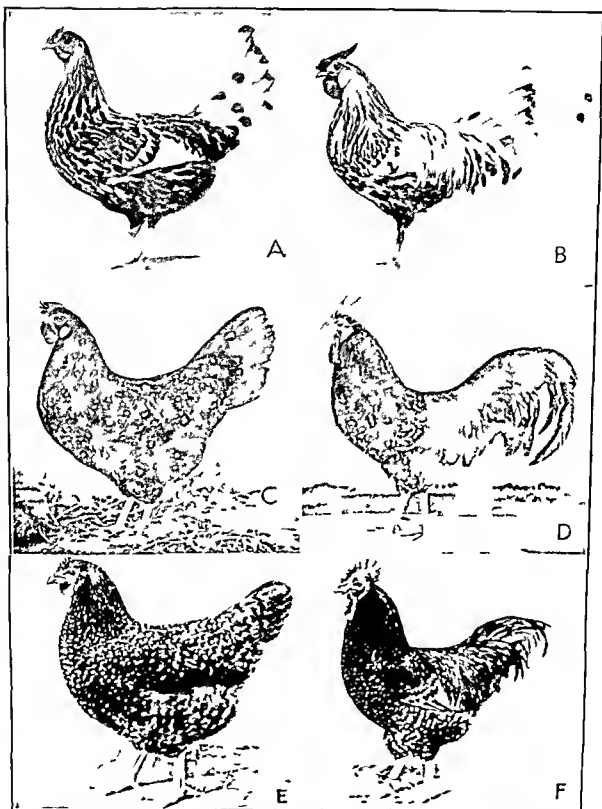
Fig 5 A and B, spangled plumage in Silver-Spangled Hamburg, C and D mottled plumage in the Ancona, E and F, white tipping at the end of the feather separated from the rest of the feather by a crescentric black bar in the Speckled Sussex (U S Dept Agr)
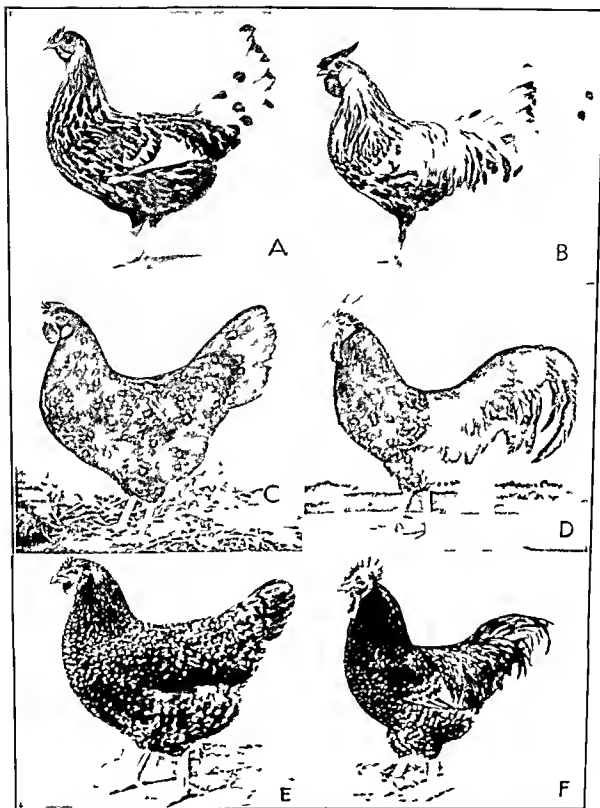
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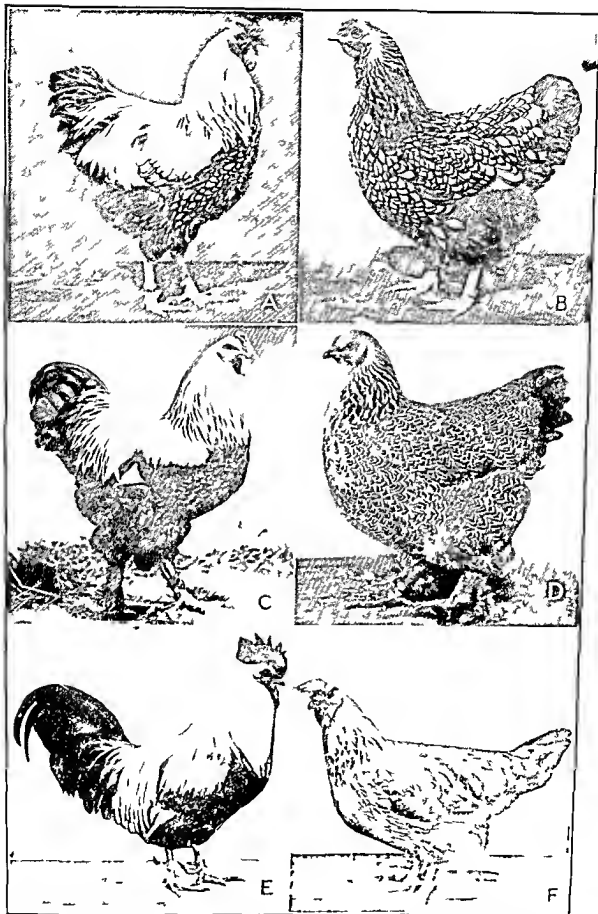
Fig 7 Sex dimorphism in plumage pattern in a laced, a penciled, and a stippled variety. A and B Silver Laced Wyandottes. C and D Dark Brahmas. E and F Silver Grey Dorkings. Except for lacing on the breast and body feathers of the Silver Laced Wyandotte male and the almost complete absence of lacing in the Silver Grey Dorking male, the three males resemble each other in appearance. B, D and F are laced, penciled and stippled respectively. (U. S. Dept. Agr.
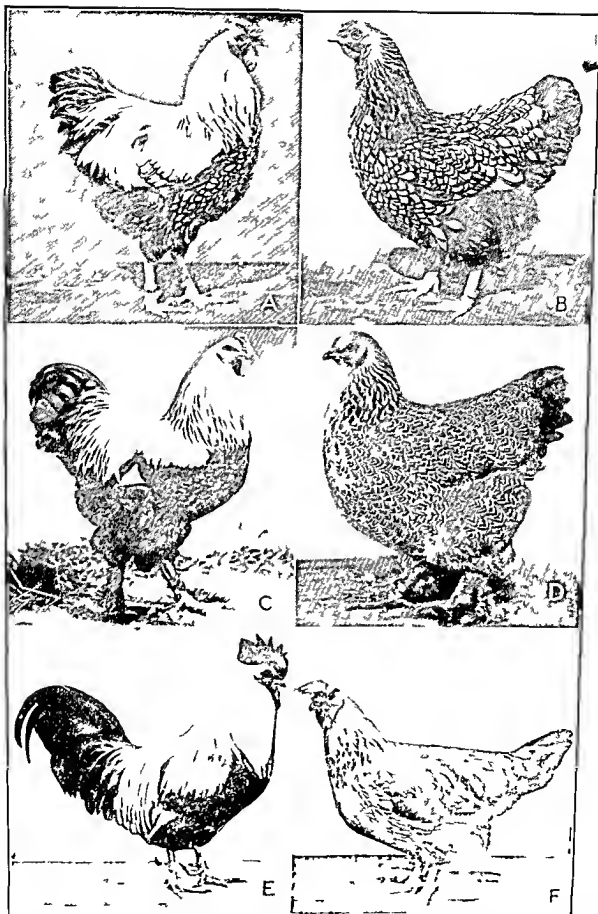
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skinned breeds   Still another factor in their favor is the absence of such adornments as crests, muffs, and feathered shanks

The Road to Further Progress. Up to the present, much has been accomplished in developing strains of different breeds and varieties to meet the needs for increased egg and meat production   Much of the progress achieved has resulted from the adoption of better husbandry practices. Some strains of broilers attain weights at 10 to 12 weeks of age undreamed of even a decade ago   Records of average egg production per bird are obtained in certain strains of layers which were formerly considered almost impossible   These are but two examples of what has been accomplished in a relatively short time, but the point should be made that such outstanding progress has been achieved by relatively few poultry breeders

What is really needed to increase greatly the efficiency of egg and poultry meat production is for *all* poultry breeders to become better informed concerning numerous breeding problems   The same point applies to hatchery operators, since they are responsible for the production of a high proportion of the chicks that are sold each year to poultry producers. In order to know *how* to develop the most intelligent selection and breeding programs, poultry breeders and hatchery operators need to be well informed with respect to *why* results are determined by certain underlying principles of reproduction. Subsequent chapters deal with these matters in detail

PROBLEMS

1. Would you care to speculate as to how the four species of wild fowl may have evolved from the ancient winged creature?

2 What are the ancestors of the domestic fowl?

3 What is the significance of "breed" in the poultry industry, and how did most of the existing breeds become established?

4 Why do you suppose so many breeds and varieties have been developed, and do you think that there is need for the development of new breeds or varieties?

5 Which of the following characters are of economic significance with respect to breeding for efficient egg and meat production type of comb, color of earlobe, color of skin, crest, number of toes, color of plumage, color of egg, and size of bird?

SELECTED LITERATURE REFERENCES

American Poultry Association, 1947 *The American Standard of Perfection* Published by the association, Davenport, Iowa

Austin, E H, 1908 Original laying capacity   *Farm Poultry* 19·347

Ball, S C, 1933 Jungle fowls from Pacific Islands   *Bull* 108. Published by Bernice P Bishop Museum, Honolulu, Hawaii

Beebe, W, 1918–1922 *A Monograph of Pheasants* Vols I–IV   H F and G Witherby, London

skinned breeds   Still another factor in their favor is the absence of such adornments as crests, muffs, and feathered shanks

The Road to Further Progress. Up to the present, much has been accomplished in developing strains of different breeds and varieties to meet the needs for increased egg and meat production   Much of the progress achieved has resulted from the adoption of better husbandry practices. Some strains of broilers attain weights at 10 to 12 weeks of age undreamed of even a decade ago   Records of average egg production per bird are obtained in certain strains of layers which were formerly considered almost impossible   These are but two examples of what has been accomplished in a relatively short time, but the point should be made that such outstanding progress has been achieved by relatively few poultry breeders

What is really needed to increase greatly the efficiency of egg and poultry meat production is for *all* poultry breeders to become better informed concerning numerous breeding problems   The same point applies to hatchery operators, since they are responsible for the production of a high proportion of the chicks that are sold each year to poultry producers. In order to know *how* to develop the most intelligent selection and breeding programs, poultry breeders and hatchery operators need to be well informed with respect to *why* results are determined by certain underlying principles of reproduction. Subsequent chapters deal with these matters in detail

PROBLEMS

1. Would you care to speculate as to how the four species of wild fowl may have evolved from the ancient winged creature?

2 What are the ancestors of the domestic fowl?

3 What is the significance of "breed" in the poultry industry, and how did most of the existing breeds become established?

4 Why do you suppose so many breeds and varieties have been developed, and do you think that there is need for the development of new breeds or varieties?

5 Which of the following characters are of economic significance with respect to breeding for efficient egg and meat production type of comb, color of earlobe, color of skin, crest, number of toes, color of plumage, color of egg, and size of bird?

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2 · Physiology
of Reproduction

Reproduction in chickens involves the mating of the sexes in order that male and female reproductive cells may unite to produce a new generation of birds. The reproductive cells are produced by gonads. The male gonad is the testicle, which produces spermatozoa (singular, spermatozoon). The female gonad is the ovary, which produces ova (singular, ovum).

Another very important function of the gonads is to secrete hormones, which are necessary for the normal development and functioning of various body structures. The sex glands, or gonads, are called endocrine glands, and they secrete male and female sex hormones, respectively.

Besides the male and female sex hormones, numerous other hormones are secreted by other endocrine or ductless glands. All the endocrine glands extract materials from the blood stream and convert them into hormones, which are distributed by the blood to various parts of the body. Hormones not only control the functioning of the ovary and testes but also influence the development of the comb, spurs, broodiness, molting, rate of body growth, feather growth and pigmentation, and various other characteristics. Taken collectively, the hormones not only regulate various processes that take place within the body but also are essential for the maintenance of life. For these reasons, the endocrine glands and the hormones they secrete are discussed first. This discussion is followed by a study of the male and female reproductive systems, including comments on the influence of certain hormones on the development of spermatozoa and ova and the production of semen. Particular attention is given to the extremely interesting endocrine regulatory mechanism involved in the release of ova from the ovary and the rhythm of laying.

ENDOCRINE REGULATORY SYSTEM

The endocrine glands, also known as glands of internal secretion, include the following: ovary, testes, thyroids, parathyroids, adrenal, "islets of Langerhans" of the pancreas, pineal, thymus, and pituitary or hypophysis.

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hormones Adrenalin has marked vasoconstrictor properties and is commonly used as an extract to raise blood pressure and as a heart stimulant There are probably several types of cortical hormones They serve in maintaining the sodium and potassium balance and facilitate the conversion of nonsugars (mainly proteins) into carbohydrates, replenishing the glycogen reserve in the body The cortical hormones are also of importance in maintaining the body's resistance to shock The normal functioning of the adrenal gland is controlled by the anterior pituitary The adrenal secretes relatively small amounts of androgen and estrogen According to Herrick and Finerty (1940), adrenalectomy results in a marked decrease in the size of the testes by way of the anterior pituitary, and, according to Kar (1947a), castration results in an increase in the amount of androgen secreted by the adrenal cortex

"Islets of Langerhans" Secretion. Certain tissues in the pancreas, the "islets of Langerhans," secrete a hormone, insulin, which influences the amount of sugar in the blood

Pineal and Thymus Endocrine functions have been attributed to the pineal and thymus glands, but practically nothing is known concerning their significance in avian physiology The pineal gland is a small, reddish gray structure attached by a stalk to the roof of the third ventricle near the junction to the midbrain The thymus is a flattened structure extending throughout the cervical (neck) region According to Latimer (1924), a regression of the thymus gland in chickens begins at about 4 months of age Greenwood (1930) observed that surgical removal of the testes and ovary causes a delay in the involution of the thymus

Pituitary Secretions. The pituitary gland, or hypophysis, is often referred to as the master gland of the endocrine regulatory system In an adult chicken, the gland is about the size of a kernel of wheat It is located beneath the floor of the brain, to which it is connected by a stalk It consists of two secretory parts, the anterior and posterior lobes

Anterior Pituitary Secretions The anterior pituitary secretes at least six recognized hormones, three of which have specific effects on the gonads

In the female, the follicle stimulating hormone (FSH), also called gonadotropin, stimulates the growth of ovarian follicles and transforms the ovary from its quiescent state to that characteristic of the normally laying hen In the male, the follicle stimulating hormone brings about testicular growth The luteinizing hormone (LH), or interstitial cell-stimulating hormone (ICSH), causes stimulation of the interstitial cells in the ovary and testes and is apparently the hormone that brings about ovulation in the hen Also, it may participate in bringing about forma-

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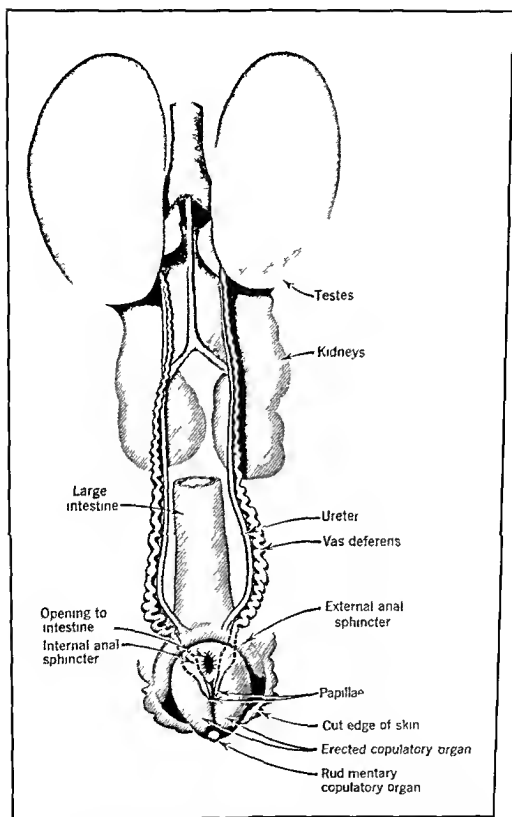
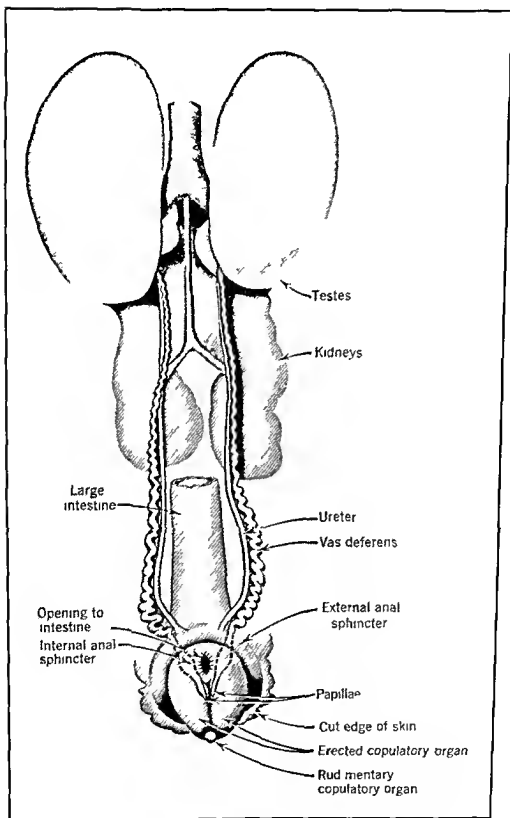Fig 8   The reproductive system of the male   (Burrows and Quinn 1937)

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to less than 1 hour of light daily and 12 hours of light daily   The maximum response in increase in size of testes in the birds exposed to light for 12 hours daily was obtained between about 2 weeks and 1 month   Increasing the daily period of light resulted in an increase in the amount of gonadotropic hormone secreted by the anterior pituitary

Incidentally, it may be pointed out here that increase in comb size in growing cockerels is the result of increased androgen secretion by the developing testes

Each testis is composed of innumerable seminiferous tubules in which the process of formation of spermatozoa or spermatogenesis yields sperms, which subsequently become spermatozoa   Macartney (1942) observed a diurnal rhythm in spermatogenesis and suggested that the time of feeding the birds is involved   For a discussion of the endocrinology of spermatogenesis in chickens, see Kumaran and Turner (1949*a*, 1949*b*, 1949*c*, 1949*d*)

The spermatozoa migrate from the seminiferous tubules of the testis to the exeurrent ducts of the small epididymis, which lies adjacent to the testis   From the epididymis the spermatozoa enter the vas deferens, which extends from the epididymis to the cloaca   According to Munro (1938), the spermatozoa are not stored in the epididymis and remain in the vas deferens for a relatively short period of time, although Burrows and Quinn (1939) have suggested that semen containing the spermatozoa is stored temporarily in the cloaca   From the cloaca the semen passes through a small hole in each of two papillae   Besides the papillae, there is a rudimentary copulatory organ   At copulation time, the semen is ejected through the holes in the papillae by the action of an anal sphincter muscle (see Fig 8)   Kosin (1942) observed precocious sexual development in Barred Plymouth Rock chicks following the injection of an androgenic agent, testosterone propionate, into the pectoral muscle of the papillae   Combs and wattles became enlarged, and crowing was noticed at 3 days of age   Kosin's findings support the observation of Macdonald and Taylor (1933) that the papilla of the male chick possesses some histological characteristics of a true penis

Each spermatozoon has a highly specialized structure consisting of a pointed aerosome on the anterior tip of the slender head, which contains the nucleus, a middle piece posterior to the head, and a long tail or flagellum   The number of spermatozoa per unit volume of semen has been determined by several investigators (Hutt 1929, Parker, McKenzie and Kempster 1942*a*, Wheeler and Andrews 1943), the number being quite variable but ranging mostly between a few hundred thousand to over 10,000,000 per cubic millimeter of semen

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The rate of semen production is influenced to some extent by the temperature in which the males are kept, it already having been noted that testicular growth is greater in young cockerels kept in a temperature of about 80° F than in young cockerels kept in a temperature of about 40° F Semen production also increases under the influence of lighting up to 12 hours daily, as shown by Lamoreux (1943*b*), maximum response to stimulation being attained in about 1 month

Semen production varies seasonally Parker and McSpadden (1943*a*), with Rhode Island Reds, showed that the time of the year during which daylight increases results in increased activity of the testes by means of the gonadotropic hormone secreted by the anterior pituitary, increased amounts of androgenic hormones being secreted by the testes Wheeler and Andrews (1943), with Barred Plymouth Rocks, also secured results indicating a seasonal influence on semen production Relatively, the largest volumes of semen were produced between November and March, and the total number of spermatozoa per ejaculation increased significantly between December and April

The results of a few investigations have shown that when males are restricted in their feed supply, semen production tends to be reduced Lamoreux and Jones (1942) and Searcy and Andrews (1943) found that dubbing the combs of males (to avoid freezing) did not affect semen production

Relatively little work has been done to determine the effect of various factors on semen quality Sampson and Warren (1939) found that in semen produced by their White Leghorn males there were relatively few morphologically defective spermatozoa The effects of hypothyroidism on semen volume and quality were studied by Shaffner and Andrews (1948) Thiouracil, a thyroid depressant was fed at 0 2 and 0 5 per cent levels, respectively, in the ration for a period of 18 weeks to two groups of sexually mature Barred Plymouth Rock males, and untreated control males were kept for observation The induced hypothyroidism did not influence sperm concentration or number of spermatozoa markedly but lowered initial motility of the spermatozoa and decreased their survival time at 40 2° F The most striking effect resulting from hypothyroidism was the reduction of fertility following a single insemination of semen

Shaffner (1948) studied the effects of hyperthyroidism through feeding thyroprotein at the rate of 10 grams per 100 pounds of feed for 16 weeks to 2-year old Barred Plymouth Rock males and found that the volume and concentration of semen were not affected but there was deterioration in semen quality and, hence, lowered fertility Huston and Wheeler (1949) compared results secured from two groups of Rhode Island Red

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of the oviduct in 26 minutes except when a yolk is in the albumen-secreting portion of the oviduct or a fully formed egg is in the uterus Although spermatozoa are able to traverse the oviduct this quickly, many of them apparently remain in folds of the oviduct for some time, according to Walton and Whetham (1933) Payne (1914) killed different females at intervals of 30 minutes to 56 days after they had been mated and observed spermatozoa in the oviducts at all periods He also observed, however, that most of the spermatozoa had lost their tails and had degenerated to a considerable extent Warren and Kilpatrick (1929) found that most spermatozoa lose their tails within 24 hours after being deposited in the female cloaca

Although only one spermatozoon fertilizes the germinal disc of the ovum, the large numbers of spermatozoa produced by males daily are necessary to secure good fertility among eggs produced during the breeding season Hutt (1929) and Sampson and Warren (1939) observed that the concentration of spermatozoa in semen bore no relation to fertilizing capacity In the artificial insemination of females, Munro (1938) suggested that about 100,000 000 spermatozoa must be inseminated in order to secure optimum fertility

Van Drimmelen (1945) artificially inseminated virgin pullets and up to the fourteenth day thereafter observed that their oviducts contained active and morphologically normal spermatozoa in the anterior end of the oviduct Eight days after semen was placed in the body cavity of virgin pullets, Van Drimmelen (1946b), observed "sperm nests" or concentrations of spermatozoa in crypts at the anterior end of the oviduct

Where Fertilization Occurs Harvey (1651), Ivanov (1924), and Vermeulen (1929) were of the opinion that fertilization took place in the ovary, before the yolk was released from the ovary On the other hand, several investigators, including Barfurth (1896), Walton and Whetham (1933), and Van Drimmelen (1946a, 1946b) were of the opinion that fertilization takes place soon after the yolk was released from the ovary

Olsen (1942) was of the opinion that fertilization normally occurs about 15 minutes after the yolk is released from the ovary Olsen and Neher (1948) demonstrated in a unique series of experiments that the ovum is normally fertilized after its release from the ovary Ova removed from ovaries of artificially inseminated pullets when transferred to oviducts of virgin pullets yielded no fertile eggs Ova removed from ovaries of virgin pullets transferred to oviducts of artificially inseminated pullets yielded fertile eggs Fertile eggs were obtained when fresh semen was placed into the anterior end of the oviduct and in the "ovarian pocket" of the body, into which yolks drop if not engulfed

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If the left ovary is surgically removed when the female chicken is a
few days old, the rudimentary right gonad develops into what is known
as a pseudotestis   The removal of the left ovary is called sinistral
ovariotomy, it causes the females (poulards) to acquire plumage re-
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Domm and Blivaiss (1947) have shown that successive implantations of
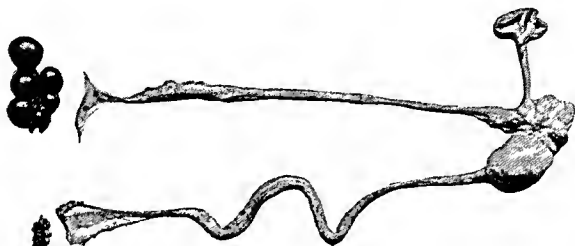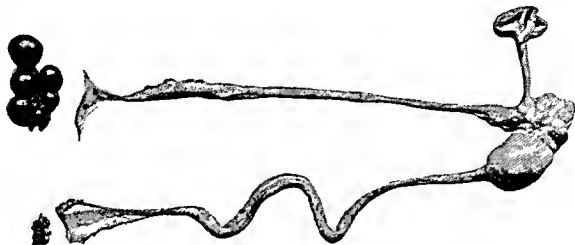androgen pellets in Brown Leghorn pullets resulted in their assuming
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FIG 10   Two ovaries and oviducts in a Rhode Island Red hen that had been laying
Note fully formed egg in uterus of lower oviduct and yolks in varying stages of de
velopment in upper ovary   At upper right the digestive tract has been severed
(B Alder, 1931)

Growth of the Ovum   In an inactive condition the ovary appears as a
small, whitish mass of irregular contour, whereas in the active condition
it appears as a yellowish cluster of spheres of varying sizes   These
spheres are ova

As growing pullets approach sexual maturity, estrogen secreted by
the ovary raises the level of lipids or fatty materials in the blood stream
as shown by Lorenz, Chaikoff, and Entenman (1938)   Thus, estrogen
secretion makes possible the deposition of yolk material in the devel-
oping follicle   Lorenz (1939) has shown that the amount of fatty acids
in the blood of hens in laying condition is several times that of immature
pullets, and Chaikoff, Lorenz, and Entenman (1941) have shown that,
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shown by the extensive observations of Marza and Marza (1935), yellow yolk as well as white yolk being secreted. According to Lillie (1919), the layers of white yolk are thinner than the layers of yellow yolk. Based on the observations of Conrad and Warren (1939), the deposition of yellow yolk is determined by the presence of xanthophyll, a carotinoid pigment, contained in the feed. When laying hens are kept in confinement and are fed a uniform diet, the yolk secreted is
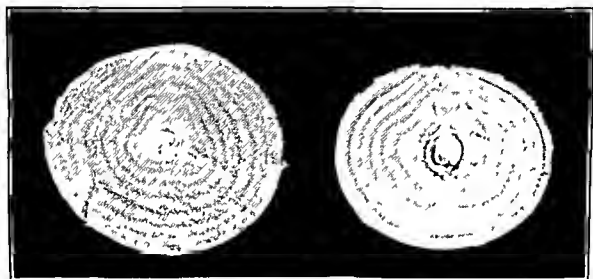

FIG. 12. Two yolks showing alternate layers of white and yellow yolk in concentric rings except where they terminate to form the neck of the latebra, which leads to the latebra in the center of the yolk. (Warren and Conrad, 1939.)

uniform in color. Apparently the yolk obtains very small amounts of carotinoid pigment from the tissues of the laying hen.

The yolk material is conveyed to the ovum by the highly vascular follicle and enters by diffusion. Romanoff (1931) has shown that the growth of the ovum is marked by a very rapid increase in the percentage of dry matter, which reaches the highest point in the mature ovum. Originally the germinal disc, or nucleus, is in the center of the ovum, but as the ovum grows through the accumulation of yolk material the germinal disc migrates to the uppermost periphery of the ovum and lies beneath the vitelline membrane. Warren and Conrad (1939) and Romanoff (1943), among others, have shown that the alternate layers of white yolk and yellow yolk are arranged nearly symmetrically except at the location of the germinal disc and where the neck of the latebra extends from below the germinal disc to the latebra in the center of the yolk (see Fig. 12). The layers of yellow yolk may be up to five times as thick as the layers of white yolk.

Each ovum grows very slowly up to about 10 days before it is ready to leave the ovary. Warren and Conrad (1939) observed that during

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Fig. 12. Two yolks showing alternate layers of white and yellow yolk in concentric rings except where they terminate to form the neck of the latebra, which leads to the latebra in the center of the yolk. (Warren and Conrad, 1939.)

uniform in color. Apparently the yolk obtains very small amounts of carotinoid pigment from the tissues of the laying hen.

The yolk material is conveyed to the ovum by the highly vascular follicle and enters by diffusion. Romanoff (1931) has shown that the growth of the ovum is marked by a very rapid increase in the percentage of dry matter, which reaches the highest point in the mature ovum. Originally the germinal disc, or nucleus, is in the center of the ovum, but as the ovum grows through the accumulation of yolk material the germinal disc migrates to the uppermost periphery of the ovum and lies beneath the vitelline membrane. Warren and Conrad (1939) and Romanoff (1943), among others, have shown that the alternate layers of white yolk and yellow yolk are arranged nearly symmetrically except at the location of the germinal disc and where the neck of the latebra extends from below the germinal disc to the latebra in the center of the yolk (see Fig. 12). The layers of yellow yolk may be up to five times as thick as the layers of white yolk.

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A day's interval between clutches is due to a postponement of ovulation The yolk of the first egg of a clutch has a longer total growth period than that of succeeding eggs in a clutch Among hens pausing 1 day between clutches, Fraps (1942) demonstrated that the enforced premature ovulation of the first yolk of the succeeding clutch by as much as 3 to 6 hours results in the premature laying of the last egg of the preceding clutch by approximately the same time

Development of Oviduct In young pullets, as long as the ovary remains relatively undeveloped and in a quiescent state, the oviduct remains relatively undeveloped Goodale (1916) was among the first to show that the surgical removal of the ovary causes the oviduct to become infantile in character This finding was confirmed by Domm (1924) Juhn and Gustavson (1930) observed that daily injections of female sex hormones into young pullets caused an increase in the functional development of their oviducts by as much as about ten times over the oviducts of untreated chicks Greenwood and Blyth (1938)

Fig 14 Left a functional ovary showing gradations in size of ova (Warren and Conrad 1939) Right A a follicle about 26 hours before the follicular rupture is to occur The stigma is narrow and the blood vessels are prominent Right B follicle immediately before rupturing the stigma is wide and the blood vessels are less prominent (Phillips and Warren 1937)

clutch, depending upon the inherent laying ability of the hen Very poor layers may skip 3 or more days before starting the next clutch and each clutch is usually not more than two eggs Good layers usually lay in clutches of three or four eggs and the intervals between clutches are usually not more than 1 day Very good layers usually lay for several days in succession one of the longest clutches on record being that of a White Leghorn that laid 223 eggs in as many days in an officially conducted Canadian egg laying contest

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Following these early reports, many others have been presented that show the dependence of the functional activity of the oviduct upon estrogens secreted by the ovary. Among these might be mentioned the increase in oviduct weight up to 80 times that of normal female chicks in chicks injected with female sex hormone, as reported by Munro and Kosin (1943). Also, Herrick (1944) injected White Leghorn female chicks between 18 and 38 days of age with a female sex hormone and observed that the development of their oviducts was more than 48 times the extent of the development of oviducts of comparable untreated chicks.

It is clear, therefore, that as the growing pullet attains sexual maturity the estrogen secreted by the ovary stimulates the functional activity of the oviduct.

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As the yolk with its gelatinous envelope of thick white progresses through the isthmus of the oviduct, some of the thick white becomes
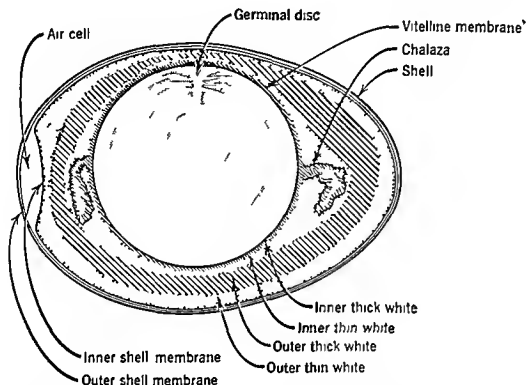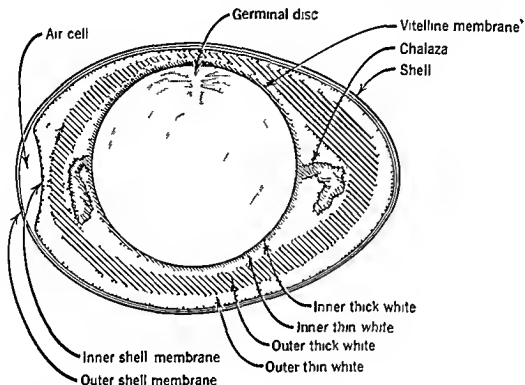

Fig 16 Schematic representation of the structure of a hen s egg All the principle parts are named except the bloom, or cuticle, on the outside of the shell and the concentric layers of white and yellow yolk forming the yolk The flask shaped structure approximately in the center of the yolk is the latebra and is comprised of white yolk The germinal disc, at the top of the neck of the latebra in a fertile incubated egg develops into the blastoderm which in turn becomes the embryo (Modified from Schaible Davidson and Moore, and Adamstone and reproduced by permission of McGraw Hill Book Co Inc, from *Poultry Husbandry* by M A Jull)

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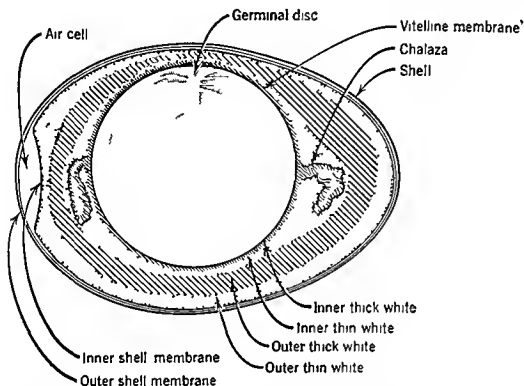through the isthmus of the oviduct, some of the thick white becomes

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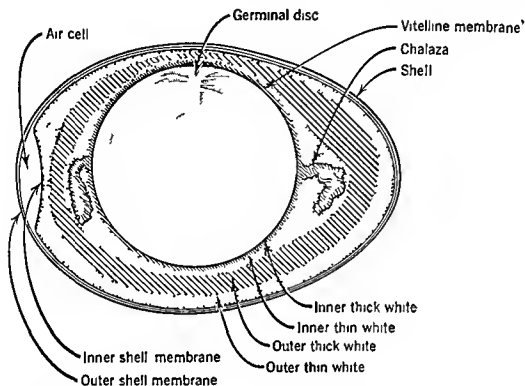

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cent magnesium carbonate, 1 per cent calcium phosphate, and 4 per cent organic material, chiefly protein. Burmester, Scott, and Card (1939) found that the rate of deposition of calcium carbonate is slow during the first 3 hours after the egg enters the oviduct but then increases and very soon attains a constant rate, which is maintained until the twentieth hour. It has been well established that the blood calcium is higher in laying birds than in nonlaying birds.

The shell is quite porous and is comprised of an inner layer of calcite crystals and a chalky layer that comprises about two-thirds of the entire shell. The porous nature of the shell and shell membranes permits the embryo to respire by the outward diffusion of carbon dioxide and the inward diffusion of oxygen. Stewart (1935) described in detail the structure of the shell of the hen's egg.

Oviposition. The act of laying requires a few minutes only, the completed egg passing from the uterus through the vagina and being expelled by the eversion of the cloaca.

Olsen (1942) observed that, within 4 hours after the yolk enters the uterus, cell division of the blastodisc has proceeded to approximately the 256-cell stage. Among eggs laid by virgin hens, Kosin (1945) found evidence of cell division in the blastodiscs, cell division apparently having ceased shortly after oviposition.

It has been indicated quite clearly that there is a relationship, apparently hormone in nature, between ovulation and oviposition. Rothchild and Fraps (1944a) surgically removed the ruptured follicle whose yolk was still in the oviduct and observed that the oviposition of the egg containing this yolk was usually delayed up to 7 days later than oviposition would normally have taken place.

Neher, Olsen, and Fraps (1950) removed mature follicles from ovaries 15 minutes after oviposition of the preceding egg of the same clutch and placed them in a warm porcelain dish, containing Ringer's or saline solution and maintained at approximately 107° F. All follicles studied were either second or subsequent follicles in their respective clutches. The follicles of hens laying two eggs per clutch ovulated in 60.5 minutes, on the average, after oviposition of preceding egg, and the follicles of hens laying three eggs per clutch ovulated in 41.7 minutes, on the average, after oviposition of preceding egg.

Burrows and Byerly (1942) injected pituitrin intravenously into hens and observed that eggs could be expelled prematurely any time after they had entered the uterus. Burrows and Fraps (1942) found that premature oviposition of hard-shelled eggs can apparently be effected by vasopressin alone, but oxytocin also is a contributing factor if administered in sufficiently high concentrations.

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Fraps, Neher, and Rothchild (1947) confirmed McNally's observation concerning the influence of activity on oviposition and, in addition, concluded that photoperiodicity is not a necessary factor in regulating oviposition Data pertaining to their results are given herewith

Feeding Time	Active Period	Eggs Laid in Active Period, per cent
Continuous	6 A M –8 P M	98
8 A M –4 P M	6 A M –6 P M	95
8 P M –4 A M	6 P M –6 A M	72

PROBLEMS

1 What principal functions are performed by estrogens and androgens?

2 What hormone is secreted by the thyroid and how is the functioning level of the thyroid regulated?

3 Mention three hormones secreted by the anterior pituitary which have specific effects on the gonads and discuss briefly the function of each of these three hormones

4 Draw an illustration of the male reproductive system and tell how spermatozoa are formed and how they are transported to the rudimentary copulatory organ

5 Mention the various factors that affect semen production and quality

6 Where does fertilization of the ovum take place?

7 Draw an illustration of the left ovary and oviduct, mentioning the different sections of the oviduct

8 Describe briefly the growth of the ovum

9 Define ovulation and oviposition and discuss briefly the relationship between the two events

10 Discuss the more important events in the formation of the four layers of albumen

11 How do light and activity influence egg laying?

12 What changes take place in a male upon being castrated and what changes take place in a female when her left ovary is removed?

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3 · Mechanism
of Inheritance

In all the higher forms of animal species, life is perpetuated through the egg. The mating of a male and female fowl serves the purpose of bringing together the male and female reproductive cells, spermatozoa and ova, respectively. It has been pointed out in the previous chapter that an ovum is fertilized by one spermatozoon only, so far as is known.

Gametes and Zygotes. From the standpoint of reproduction and inheritance, the reproductive cells are spoken of as "gametes," the term "gamete" meaning a spouse. The ovum is the female gamete and the spermatozoon the male gamete. The fertilization of the female gamete by the male gamete produces the fertilized egg, which is spoken of as the "zygote," a term meaning yoked together. It is the zygote that develops into the chick.

Chromosomes. Each gamete contains little threadlike bodies called "chromosomes," which are transmitted from parent to offspring. A fact of fundamental importance is that the number of chromosomes in any given species of animal is constant. The number of chromosomes in the domestic fowl has been studied by a number of investigators, several of whom observed a relatively large number, a few being large and several being very small. Yamashina (1944) concluded that the female chicken has 77 chromosomes and the male chicken 78 chromosomes.

Sex Chromosomes and Autosomes. The difference between the number of the chromosomes in the male and female is due to the fact that the female has one less chromosome than the male. The sex chromosomes in any species apparently are always associated with sex. The female chicken has 1 sex chromosome and the male has 2 sex chromosomes. The rest of the chromos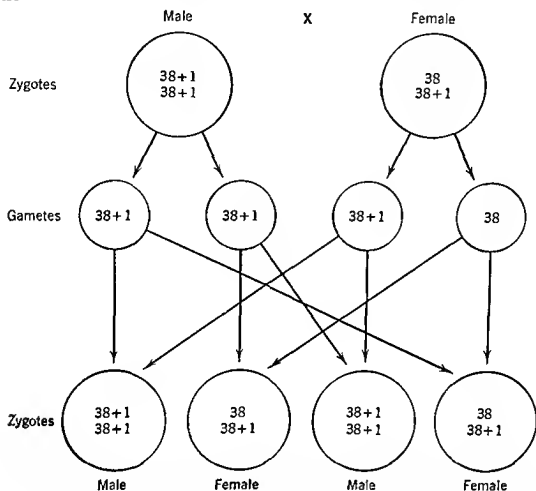omes are called "autosomes" and are always in pairs. According to Yamashina, the male has 38 pairs of autosomes and 2 sex chromosomes, whereas the female chicken has 38 pairs of autosomes but only 1 sex chromosome (see Fig. 18).

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form of an equation, the situation is thus A gamete of male origin with 38 autosomes and 1 sex chromosome + a gamete of female origin with 38 autosomes = a zygote with 38 pairs of autosomes and 1 sex chromosome
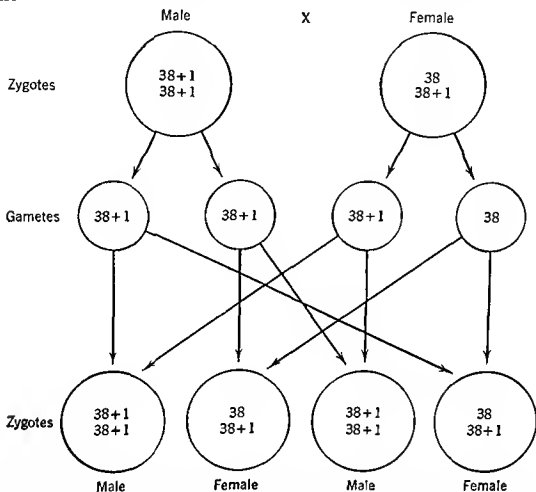

Fig 19 The male fowl has 38 pairs of autosomes plus 1 pair of sex chromosomes whereas the female fowl has 38 pairs of autosomes but only 1 sex chromosome The male produces but one kind of gametes each of which contains 38 autosomes plus 1 sex chromosome The female produces two kinds of gametes one kind containing 38 autosomes plus 1 sex chromosome and the other containing 38 autosomes but no sex chromosome A gamete of male origin upon uniting with the gamete of female origin containing the sex chromosome produces a zygote containing 38 pairs of autosomes plus 1 pair of sex chromosomes such a zygote develops into a male A gamete of male origin upon uniting with the gamete of female origin containing no sex chromosome produces a zygote containing 38 pairs of autosomes but only 1 sex chromosome such a zygote develops into a female

Up to the present only one phase of the reproductive cycle has been discussed, the union of a gamete of paternal origin with a gamete of maternal origin The other phase of the reproductive cycle consists in the development of the gametes from the zygotes For the sake of simplicity, the behavior of the sex chromosomes in the processes involved is omitted from this brief discussion Each zygote gives rise to

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acter confined exclusively to birds, but the fact that some birds have laced feathers whereas other birds have penciled feathers and the fact that some birds lay well whereas others do not are matters that require explanation if one is to gain a clear understanding of the manner in which the different characters that birds possess are reproduced from one generation to the next From the standpoint of inheritance, the term character means any one of the many details of form, substance, structure, or function in a fowl's make-up

Inheritance is transmission from parent to offspring The characters are not transmitted bodily, however, for instance, there are no feathers in the egg or on the chick when hatched, but the chick possesses the ability to grow feathers It is the ability, power, or potentiality to develop characters, such as white or yellow skin color, barred or spangled feathers, crests, feathered shanks, brown or white color of egg shell, that is inherited It is the ability to produce an abundant amount of flesh of excellent quality or the ability to lay well that is inherited

Although it is true that the characters which a fowl possesses are not transmitted bodily, it seems justifiable to speak of the inheritance of characters, as, for instance, the inheritance of white and black, of barring, and of egg production Such a method of discussing the subject of inheritance simplifies the problem of presenting the matter

The Significance of Variation Reference has already been made to numerous characters possessed by domestic fowls, but the fact should be emphasized here that each and every individual fowl possesses a large number of characters A Barred Plymouth Rock possesses a single comb, barred feathers, red earlobes, yellow skin, beak, and shanks, nonfeathered shanks, and four toes, as well as many other characters A Light Brahma possesses a pea comb, a columbian colored plumage pattern, and feathered shanks and has a different shape from that of the Barred Plymouth Rock A White Plymouth Rock, however, has the same shape as the Barred variety but differs from it in having white plumage Moreover, not all White Plymouth Rocks are exactly alike There is always some difference, however minute that distinguishes two individuals which are otherwise much alike, and this is as true among men as among domestic fowls

It should be kept in mind, of course, that conditions under which birds are kept (their environment) sometimes exert a considerable influence on various hereditary characters, such as growth and egg production Disease and parasites usually increase the amount of variation that normally exists among individuals in a flock For further information on the relationship between heredity and environment the reader should consult Dobzhansky (1950)

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The Significance of Variation. Reference has already been made to numerous characters possessed by domestic fowls, but the fact should be emphasized here that each and every individual fowl possesses a large number of characters. A Barred Plymouth Rock possesses a single comb, barred feathers, red earlobes, yellow skin, beak, and shanks, nonfeathered shanks, and four toes, as well as many other characters. A Light Brahma possesses a pea comb, a columbian colored plumage pattern, and feathered shanks and has a different shape from that of the Barred Plymouth Rock. A White Plymouth Rock, however, has the same shape as the Barred variety but differs from it in having white plumage. Moreover, not all White Plymouth Rocks are exactly alike. There is always some difference, however minute, that distinguishes two individuals which are otherwise much alike, and this is as true among men as among domestic fowls.

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The manner in which the characters black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams will serve to illustrate the mechanism involved in the inheritance of many pairs of characters The first reference to a cross of this type which had actually been made was reported by Bateson and Punnett (1908) They mated Black Rose-Comb Bantams to White Rose Comb Bantams and secured black progeny only They mated 3 of the F_1 black females to 1 of the F_1 black males and secured 70 black and 24 white progeny This result approximates very closely a ratio of 3 blacks to 1 white

The results of crosses between White Rose-Comb and Black Rose-Comb Bantams secured at the U S Animal Husbandry Experiment Farm, Beltsville, Maryland, are given, in Table 1, together with photographs of birds used in the various matings (see Figs 20 and 21)

Dominance and Recessiveness. It has already been noted that in the cross between Black Rose-Comb and White Rose-Comb Bantams all the F_1 progeny are black The gene for white was transmitted in exactly the same manner as the gene for black, but none of the F_1 birds shows any white in its plumage Each zygote giving rise to an F_1 bird contains a gene for black and a gene for white, but a black bird is the result Black is dominant to white in this particular cross The white of the White Rose-Comb Bantam is recessive to color

Since in this cross black is dominant to white the character black is represented by the capital letter N, meaning nigrant or black, and the recessive character white is represented by the small letter n, meaning the absence of nigrant or black (See Fig 22) Furthermore, since genes are responsible for the development of the hereditary characters black and white, the genes are represented by the letters N and n respectively The zygote of the purebred Black Rose Comb Bantam contains the genes NN, and the zygote of the purebred White Rose-Comb Bantam contains the genes nn

It should be pointed out that the symbols N for black and n for white are used here purely as a matter of convenience, the proper symbols that correctly express the difference between black and white plumage in Rose-Comb Bantams are given in the next chapter The symbols N and n are employed at this time for the sake of simplicity in illustrating the principle of dominance of one character over another and the principle of the segregation of characters The symbol B is not used for black because B has long since been used to represent barring.

Homozygous and Heterozygous The constitution of the zygote of the purebred black parent (NN) is spoken of as being "homozygous" which means simply that two similar genes are contained in the zygote
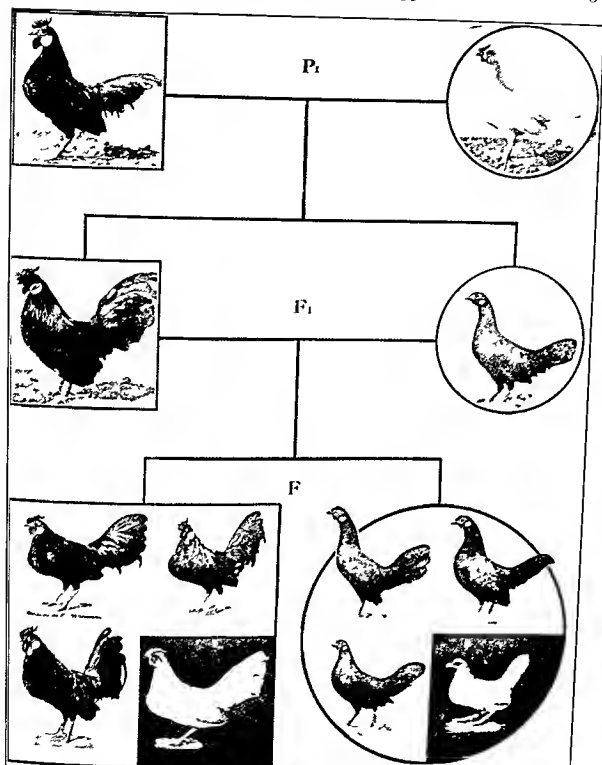
The manner in which the characters black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams will serve to illustrate the mechanism involved in the inheritance of many pairs of characters The first reference to a cross of this type which had actually been made was reported by Bateson and Punnett (1908) They mated Black Rose-Comb Bantams to White Rose Comb Bantams and secured black progeny only They mated 3 of the F_1 black females to 1 of the F_1 black males and secured 70 black and 24 white progeny This result approximates very closely a ratio of 3 blacks to 1 white

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Dominance and Recessiveness. It has already been noted that in the cross between Black Rose-Comb and White Rose-Comb Bantams all the F_1 progeny are black The gene for white was transmitted in exactly the same manner as the gene for black, but none of the F_1 birds shows any white in its plumage Each zygote giving rise to an F_1 bird contains a gene for black and a gene for white, but a black bird is the result Black is dominant to white in this particular cross The white of the White Rose-Comb Bantam is recessive to color

Since in this cross black is dominant to white the character black is represented by the capital letter N, meaning nigrant or black, and the recessive character white is represented by the small letter n, meaning the absence of nigrant or black (See Fig 22) Furthermore, since genes are responsible for the development of the hereditary characters black and white, the genes are represented by the letters N and n respectively The zygote of the purebred Black Rose Comb Bantam contains the genes NN, and the zygote of the purebred White Rose-Comb Bantam contains the genes nn

It should be pointed out that the symbols N for black and n for white are used here purely as a matter of convenience, the proper symbols that correctly express the difference between black and white plumage in Rose-Comb Bantams are given in the next chapter The symbols N and n are employed at this time for the sake of simplicity in illustrating the principle of dominance of one character over another and the principle of the segregation of characters The symbol B is not used for black because B has long since been used to represent barring.

Homozygous and Heterozygous The constitution of the zygote of the purebred black parent (NN) is spoken of as being "homozygous" which means simply that two similar genes are contained in the zygote

Fig 21 A Black Rose Comb Bantam male mated to a White Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation) all of which are black, as in the reciprocal cross illustrated in Fig 20 Similar results are secured in the F_2 generation, 3 blacks to 1 white, owing to the well-established Mendelian principle of the segregation of the genes The results secured in this cross and in the cross illustrated in Fig 20 demonstrate that the genes for black and for white are contained in the autosomes and not in the sex chromosomes See Figs 22 and 23, which show clearly how the proportion of 3 blacks to 1 white is secured in the F_2 generation of the crosses illustrated (Jull and Quinn 1929)

Fig 21   A Black Rose Comb Bantam male mated to a White Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation) all of which are black, as in the reciprocal cross illustrated in Fig 20   Similar results are secured in the F_2 generation, 3 blacks to 1 white, owing to the well-established Mendelian principle of the segregation of the genes   The results secured in this cross and in the cross illustrated in Fig 20 demonstrate that the genes for black and for white are contained in the autosomes and not in the sex chromosomes   See Figs 22 and 23, which show clearly how the proportion of 3 blacks to 1 white is secured in the F_2 generation of the crosses illustrated   (Jull and Quinn 1929)

F_1 **Black hybrid X Black hybrid**

FIG 23   The F_1 zygotes give rise to the F_1 gametes, and these gametes unite in pairs to form the F_2 zygotes, which develop into the F_2 progeny   The color of the progeny is in the proportion of 3 blacks to 1 white   Among the blacks, 1 is homozygous and 2 are heterozygous for black   The homozygous black and the homozygous white are the same kind of birds as the original parents, see P_1 zygotes in
Fig 22

FIG 24   Showing the F_2 results produced by a mating of an F_1 male $\times$ F_1 female, each of the F_1 birds being black because in this cross black is dominant to white   The F_2 generation consists in the proportion of 3 blacks to 1 white

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large enough numbers of F_2 birds are secured   This ratio is accounted for by the segregation and recombination of the genes from one generation to another

The Principle of Segregation. In the cross between two contrasting characters, black and white, it has already been observed that in the first filial generation one character dominated the other but in the second filial generation there was a segregation of the characters so that the two contrasting color characters appeared in the proportion of 3 blacks to 1 white   Two contrasting characters brought together in F_1 become separated from each other in F_2

Furthermore, it has also been observed that in the F_2 generation there are blacks that breed true, producing nothing but blacks, and whites that breed true, producing nothing but whites   There are also blacks that do not breed true, for when they are mated among themselves they produce progeny in the ratio of 3 blacks to 1 white, if sufficient numbers are raised   Therefore, although the F_2 generation is comprised of 3 blacks to 1 white, the blacks differ in respect to the results they produce when they are bred   Among every 3 blacks 1 is homozygous whereas the other 2 are heterozygous for color, so that the F_2 ratio is really 1   2   1, that is 1 homozygous for black, 2 heterozygous for black, and 1 homozygous for white, that is $1\,NN$ $2\,Nn$ $1\,nn$

The demonstration of the segregation of characters in the F_2 generation and the concurrent demonstration of the segregation of the genes as separate units comprise the first of two major contributions Mendel made to the science of breeding   The establishment of the principle of segregation gave birth to a new conception concerning the manner in which characters are inherited from generation to generation and led to remarkable discoveries concerning the mechanism of inheritance of many characters in poultry

The Principle of Independent Assortment   The second of the two major contributions Mendel gave to the science of breeding is the demonstration of the principle of the independent assortment of the genes   This principle is clearly illustrated in the case of the inheritance of two pairs of characters

The inheritance of two pairs of characters is precisely the same in principle as the inheritance of one pair   Since two pairs of characters are involved, the F_1 hybrids are able to produce four kinds of gametes instead of only two, as in the case of the inheritance of one pair of characters   Since four kinds of gametes are produced by each sex, the possibilities for the segregation and recombination of the genes is four times as great as when only two kinds of gametes are formed as shown in Fig 25

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single-comb parent produces *rn* gametes, these unite to form the F_1 zygote *RrNn* Such zygotes are heterozygous for both pairs of characters, but the presence of *R* and *N* makes the F_1 birds rose-comb black The F_1 male zygote produces four kinds of gametes (sperm) *RN, Rn, rN, rn*, and, likewise, the F_1 female zygote produces the same four kinds of gametes (eggs) *RN, Rn, rN, rn* There are sixteen possible combinations The checkerboard plan of illustrating the kind of zygote formed by the mating of any two gametes is very effective, as shown in Fig 25

The type of comb and the color of the bird arising from each of the 16 zygotes formed are given in parentheses in each square in Fig 25 Of the 16 zygotes formed, it is observed that they give rise to 9 rose comb blacks, 3 rose-comb whites, 3 single-comb blacks, and 1 single comb white, a 9 3 3 1 ratio If comb alone is considered, however, it is apparent that there are 12 rose combs and 4 single combs, a 3 1 ratio Also, if color alone is considered, it is seen that there are 12 blacks and 4 whites, a 3 1 ratio

Of the 16 F_2 birds, 12 are black, of which 9 are rose combs and 3 are single combs, a 3 1 ratio Of the 16 F_2 birds, 4 are white, of which 3 are rose combs and 1 is a single comb, a 3 1 ratio In other words for either pair of characters considered separately, a 3 1 ratio results

New Types Produced. It is interesting to observe that the mating of Black Rose-Comb Bantams and white single-comb bantams has produced in the F_2 generation four kinds of birds rose-comb blacks, rose-comb whites, single-comb blacks and single comb whites The rose-comb blacks and the single-comb whites are the same kinds as the parents, but the rose-comb whites and the single comb blacks are new types How did these new types arise?

The parental zygotes are *RRNN* and *rrnn* All the F_1 zygotes are of one kind, *RrNn* The F_2 zygotes as observed in the checkerboard, are as follows

1 *RRNN*—homozygous rose comb and homozygous black		
2 *RRNn*—homozygous rose comb and heterozygous black		9
2 *RrNN* —heterozygous rose comb and homozygous black		
4 *RrNn*—heterozygous rose comb and heterozygous black		
1 *RRnn*—homozygous rose comb and homozygous white		3
2 *Rrnn* —heterozygous rose comb and homozygous white		
1 *rrNN* —homozygous single comb and homozygous black		3
2 *rrNn* —homozygous single comb and heterozygous black		
1 *rrnn* —homozygous single comb and homozygous white		1

16   16

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1 *rrNN*—homozygous single comb and homozygous black	3
2 *rrNn*—homozygous single comb and heterozygous black	
1 *rrnn*—homozygous single comb and homozygous white	1

16   16

independent characters. It will be recalled that in the case of 1 pair of characters 2 kinds of F_1 gametes are formed and that in the case of 2 pairs of characters 4 kinds of F_1 gametes are formed. The number of different kinds of gametes formed by the F_1 birds is doubled with each increase in the number of different genes involved.

In the inheritance of 3 pairs of characters 8 kinds of F_1 gametes are formed, and in the inheritance of 4 pairs of characters 16 kinds of F_1 gametes are formed. Each time the different genes involved are increased by 1, the number of F_1 gametes formed is increased by 2. On the other hand, each increase in the number of different genes involved increases by 4 the average number of F_2 individuals required to be produced to secure the appearance of the various combinations of characters resulting from the chance combination of the different kinds of F_1 gametes.

It becomes clear, therefore, that, regardless of the number of independent characters involved in the original cross, the mode of inheritance is the same, and the different types produced in the F_2 generation always bear a certain mathematical proportion, depending upon the number of independent pairs of genes involved. It is well to keep in mind, however, that, with respect to the inheritance of such quantitative characters as growth, hatchability, and egg production, so many genes are involved that n curve representing the distribution of the F_2 generation would have relatively few individuals at each end and have increasing numbers toward the center, where the greatest numbers would appear.

Genotype and Phenotype. From the original mating of Black Rose-Comb Bantams and single-comb white bantams, F_2 zygotes were secured in the ratio of 1 *RRNN* : 2 *RRNn* : 2 *RrNN* : 4 *RrNn* : 1 *RRnn* : 2 *Rrnn* : 1 *rrNN* : 1 *rrNn* : 1 *rrnn*. Each group of zygotes represents a *genotype*, which means simply the genetic constitution of the birds with respect to comb type and plumage color.

From the standpoint of the appearance of the F_2 generation with respect to comb type and plumage color, the following ratio was secured: 9 rose-comb blacks : 3 rose-comb whites : 3 single-comb blacks : 1 single-comb white. Each of these four groups represents a *phenotype*.

Backcross, Reciprocal, and Diallel Matings. In inheritance studies, it is sometimes desirable to mate some of the progeny to one of the parents or other birds of the same genotype with respect to the character being investigated. Such a mating is called a *backcross*. An example of *reciprocal matings* is: Black Rose-Comb Bantam male × White Rose-Comb Bantam female and Whtie Rose-Comb Bantam male × Black Rose-Comb Bantam female. Another example is: Rhode Island

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takes place in the gene   Snyder (1946) pointed out that mutations are of relatively rare occurrence   This is to be expected, because most genes are exceedingly stable   The stability of genes is obvious when it is realized that birds and other domestic animals are relatively stable organisms and produce offspring that do not depart from the normal except in rare instances   As Lush (1948) has pointed out, the amount of variation among birds in a flock from one generation to the next is much the same   A dominant mutation produces its effect in the succeeding generation   A recessive mutation becomes apparent only when both parents possessing the mutation are mated together, the recessive mutation thus being in a homozygous condition   In chickens, a recessive sex-linked mutation may produce an immediate effect in the female   Most mutations are harmful, and most of them are recessive   Many mutations are lethal in their effect   An excellent discussion of mutations is given by Muller (1947b)

Phenocopies. This term refers to the simulation of gene effects by the action of extrinsic factors, a good example in birds being rumplessness resulting from some accident during the embryonic development, although this condition resembles hereditary rumplessness in certain other birds   Rumplessness can be produced by injecting insulin into the yolk sac during embryonic development, as Landauer (1948) has shown

Lethal and Sublethal Genes. An autosomal lethal gene eliminates the individual homozygous for it   When Creepers are mated among themselves, instead of the ratio of three Creepers to one normal, actually a ratio of two Creepers to one normal results in the offspring   One-fourth of the offspring, those homozygous for the Creeper gene, which is dominant, die during the first week of incubation   The markedly shortened legs of some Cornish fowl have been shown to be due to an incompletely dominant autosomal lethal gene   Embryos homozygous for this gene die during the last week of incubation, those alive at 22 days being unable to hatch   Not only are the legs of the homozygous embryos extremely short but also the beaks and wings are short and the eyes are bulging   An example of a dominant autosomal sublethal gene is one that causes almost complete absence of feathers in chicks at hatching time   Hatchability is normal, but most of the affected chicks die within 5 months after hatching

Most lethal genes are recessive, their existence being made known by hatchability records   Autosomal recessive lethals become manifest when the gene is in a homozygous state   These cases are discussed in later chapters so that at this time only a few need be cited   *bilateral microthalmia*, reduced eyeballs, ***chondrodystrophy***, a characteristic short-

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SEX-LINKED INHERITANCE

In the domestic fowl, certain characters are transmitted from the dam to her sons but not to her daughters, although the same characters are transmitted from the sire to his sons and daughters Characters that are transmitted from dam to sons only are called "sex-linked" characters

The results secured from a mating between a Rhode Island Red male and a Barred Plymouth Rock female are illustrated in Fig 26 The male progeny are barred, and the female progeny are black or largely so Some of the female progeny may have red in the neck and breast feathers, but black is the predominant plumage color

The results of a mating between a Barred Plymouth Rock male and a Rhode Island Red female are illustrated in Fig 27 All the progeny, males and females, are barred Barring is dominant to nonbarring

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Fig 27 Showing the manner in which the dominant sex linked gene *B* for barring is transmitted to the daughters as well as the sons in a mating of Barred Plymouth Rock male × Rhode Island Red female

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Barred Plymouth Rock Male   X   Rhode Island Red Female

Zygotes: $38+B$ / $38+B$ 38 / $38+b$

Gametes: $38+B$ $38+B$ $38+b$ 38

Zygotes:
$38+B$ / $38+b$ — Barred male
38 / $38+B$ — Barred female
$38+B$ / $38+b$ — Barred male
38 / $38+B$ — Barred female

Fig 27 Showing the manner in which the dominant sex linked gene B for barring is transmitted to the daughters as well as the sons in a mating of Barred Plymouth Rock male × Rhode Island Red female

uniting with the gamete of male origin containing the sex chromosome develops into a male whereas the gamete of female origin that does not contain the sex chromosome upon uniting with the gamete of male origin containing the sex chromosome develops into a female chick

Egg Characters. According to the observations of Jull (1924) and Jull and Quinn (1924, 1925), the sex ratio of chicks hatched is not in any way affected by egg shape or size or by any other physical characteristics of eggs. Several workers have shown that antecedent egg production does not influence the sex ratio

Disease. That disease may affect the sex ratio is indicated by the observation of Byerly and Jull (1935). They summarized the data of Dunn (1927), Hutt and Greenwood (1929), and Munro (1932) and their own data pertaining to embryos dying from a specific type of chondrodystrophy. Among 465 such embryos, 263 were males or 56 6 per cent. This high sex ratio in affected embryos indicates that males are more susceptible than females to this particular disease. No explanation has as yet been proposed to account for this deviation from the normal sex ratio. Hazel and Lamoreux (1946) observed a sex ratio of 49 79 among 8355 White Leghorn chicks obtained from matings designed to measure the effects of sex linked lethals upon the variation in family sex ratios. It is obvious that, in their stock, sex-linked lethals did not affect embryonic mortality

Breeds. That breeds sometimes differ with respect to their sex ratios has been reported by Callenbach (1929), Byerly and Jull (1935), and Crew (1938), all of whom found the sex ratio of Rhode Island Reds slightly higher than that of White Leghorns. Dudley and Hindbaugh (1939) observed differences in the sex ratios of different strains at hatching time

Except for the sex ratio variations due to disease or breed and strain differences just reported, the results of practically all studies on sex ratios indicate that the sex ratio of the domestic fowl is slightly below 50

At Commencement of Incubation. Hays (1945) observed that the percentage of male embryos in all fertile eggs at commencement of incubation (primary sex ratio) was 49 7 in Rhode Island Reds. Over a period of 10 years he determined the sex of chicks hatched from 39 dams all of whose eggs hatched, thus excluding the possible effects of prenatal mortality

At Hatching Time. Observations on sex ratios at hatching time (secondary sex ratios) have been numerous. In the previous edition of this book, the author summarized the results secured by fourteen different investigators involving 102,143 cases which yielded a sex ratio of 49 38. This is very close to the previously mentioned 49 79 sex ratio

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The regression of the male comb following castration is prevented by transplanting into the body cavity testis tissue obtained either from the bird operated upon or from other birds, as indicated by the results secured by Appel (1929) The restoration of the capon comb to the cock condition by the injection of testis hormone was also demonstrated by Hardesty (1931), who observed that the hormone produces its effect by stimulating the secretion of mucoid in the comb

In the female the growth of the comb is coincident with the increased activity of the ovary, the cortex of which secretes a female sex hormone whereas the medulla of the ovary secretes a male hormone, according to Greenwood and Chu (1939) As the hen approaches laying condition the comb enlarges and becomes more turgid as a result of the increased activity of the ovary, but it "lops" to one side in some breeds, owing to the asymmetrical lateral increase in the number of connective-tissue fibers The increased turgidity, though not reaching the level observed in the cock's comb, is due to the secretion of mucoid in the intermediate layer of the comb as the result of the influence of the male hormone, according to Hardesty (1931) When egg production ceases, the female comb regresses because less and less mucoid is secreted The comb of the nonlaying hen may be compared with the comb of the capon, the injection of the female hormone having practically no effect

Spurs. Most adult males, including capons, have spurs, whereas it is unusual for a female to have spurs Goodale (1916) and Domm (1927), among others, observed that spurs always develop in the female following ovariotomy, the removal of the ovary From this it appears that spurs develop best in the absence of the female gonad Kozelka (1929, 1932) has shown that the spurs from either sex grafted to the male host were of the male type, for the most part, whereas on the female host the spur retained the characteristic type of the donor Kozelka (1933) secured evidence indicating that, once the chick is hatched, the male sex hormone does not influence the female spur Apparently sex dimorphism in spur development is due primarily to a genetic difference, as observed by Goodale (1925)

Erythrocyte Count. The fact that the mature male and female fowl differ in the number of red blood corpuscles, or erythrocytes, present in the blood has been demonstrated by Chaudhuri (1927), Juhn and Domm (1930), Domm, Taber, and Davis (1943), and Domm and Taber (1946) Mature males have about 33 per cent more erythrocytes per cubic millimeter of blood than mature females Capons and poulards, sinistrally and bilaterally ovariotomized pullets, have about the same erythrocyte count as mature females
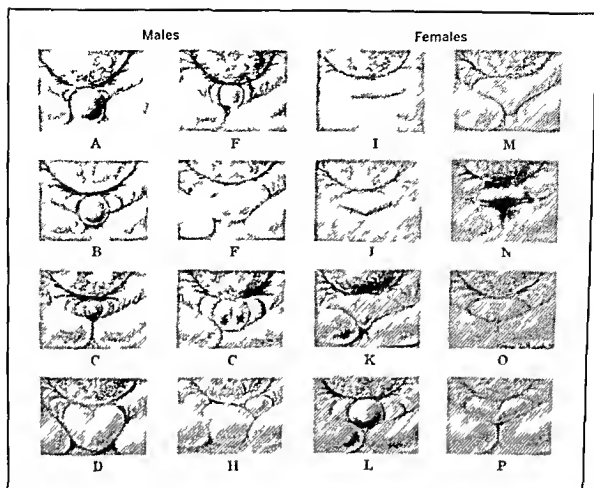
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Fig 28 Left different types of rudimentary copulatory organs in male chicks at hatching time The following are the approximate percentages of the types normally found A and B 64 C 8 E and F 21 G 3 H 35 D 05 Right different types of copulatory organs in female chicks at hatching time The following are the approximate percentages of the types normally found I and J 57 K L and M 17 N 25 O and P 1 (Canfield 1941)

gree of social dominance is determined by peck order, which serves as an index of combativeness In a small flock one hen may "boss" all the other females in the flock A state of social hierarchy usually exists among males in flock matings, also Socially dominant males and fe males naturally tend to produce relatively more offspring than other males and females Those who may be interested should consult the following references and others cited therein Allee and Collias (1940) Allee, Collias and Beeman (1940), Allee, Collias and Lutherman (1939), Collias (1943), Domm and Davis (1948), and Guhl and Warren (1946)

Plumage Types and Patterns The lower neck, saddle, and tail feathers are longer and more pointed in the male than in the female In Chapter 1 it was pointed out that sex dimorphism in plumage pattern is a characteristic feature of parti colored varieties such as the

Males — Females

A E I M

B F J N

C G K O

D H L P

Fig 28 Left, different types of rudimentary copulatory organs in male chicks at hatching time The following are the approximate percentages of the types normally found A and B, 64, C, 8, E and F, 21, G, 3, H, 3 5, D, 0 5 Right, different types of copulatory organs in female chicks at hatching time The following are the approximate percentages of the types normally found I and J, 57, K, L, and M, 17, N, 25, O and P, 1 (Canfield, 1941)

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Fig. 29. Males acquire different types of plumage under different circumstances. A, a capon, resulting from the removal of the testes. (U. S. Dept. Agr.) B, a developmental capon, no operation having been performed. (After Greenwood and Crew.) C, a Brown Leghorn cockerel that acquired plumage resembling that of a female as a result of being fed desiccated thyroid. D, a hen-feathered Brown Leghorn male, the result of breeding. E, a cock-feathered Silver-Laced Wyandotte male. F, a hen-feathered Silver-Laced Wyandotte male. (U. S. Dept. Agr.)

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quires the plumage characteristic of the capon, the ovariotomized female being called a poulard When a bilateral ovariotomy is performed before the assumption of adult female plumage, the poulard develops typical juvenile male plumage, which is subsequently replaced by adult male plumage The type of plumage developed after sinistral ovariotomy, the removal of the left ovary but not the rudimentary right gonad, varies considerably, depending upon the age at which the female is operated upon Sinistrally ovariotomized females that have acquired male-type plumage may later acquire female-type plumage, because of the influence of secretions elaborated by the enlarged rudimentary right gonad

When the ovary of a hen is transplanted into a capon, the capon-type plumage reverts to the female type, although Domm (1939) points out that such feminized capons ultimately revert more or less completely to the capon type of plumage

Bilaterally ovariotomized females into which have been transplanted testicular grafts retained the male type of plumage characteristic of the typical cock

The results of these experiments demonstrate that the testicular hormone does not modify the male or female plumage of cock-feathered breeds and that the female hormone elaborated by the ovary suppresses male plumage It has also been shown that, when an adult female is sinistrally ovariotomized, she acquires male-type plumage, which subsequently reverts to female-type plumage as a result of a female hormone elaborated by the hypertrophied rudimentary right gonad

PROBLEMS

1 Of what significance, in selection and breeding programs is the fact that there is considerable variation with respect to most characters which chickens possess?

2 How could you determine whether the variability of a character is due primarily to genetic or environmental influences?

3 How is it that individuals that look very much alike sometimes give quite different results in breeding?

4 What is the significance of the segregation and independent assortment of the genes in inheritance?

5 Define each of the following terms and give an illustration of the proper use of each term gene, gamete, zygote genotype phenotype, hemizygous homozygous, heterozygous allelomorph, modifying genes, epistatic genes, lethal genes, cryptomere

6 How could you determine whether new characters are mutations or the result of segregation and recombination of genes following certain matings?

7 What practical use can be made of sex linked inheritance?

8 Give three examples of sex dimorphism in chickens other than with respect to plumage pattern

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4 · Color Characters

Color characters are among the most conspicuous of all the characters that domestic fowls possess Plumage color characters constitute the basis for differentiating the varieties of a breed Color characters include skin color, earlobe color, shank color, down color of chicks, adult plumage color, and egg-shell color, a discussion of the last character being reserved for the chapter "Egg Characters"

Since most poultry breeders are not interested in the breeding of the numerous parti-colored breeds and varieties with their great array of color patterns, a review of investigations on plumage color inheritance must be brief in a book of this kind Moreover, comparatively little is known concerning the inheritance of the more complicated plumage patterns in the laced and penciled varieties and other varieties in which three or more colors make up the plumage pattern In addition, recent research on the influence of hormones on feather pigmentation indicates quite clearly that much more attention must be given to the physiology of feather pigmentation before marked advances can be expected in determining the genetics of some plumage patterns

For a clear understanding of the various factors involved in plumage pigmentation and plumage patterns, it is necessary to have some understanding of feather growth and structure and how feathers become pigmented

FEATHER DEVELOPMENT AND PLUMAGE PIGMENTATION

Each feather begins its growth in a follicle, a depression in the skin of the embryo These follicles develop before hatching time and give rise to chick down Later, as the true feather arises from the follicle, the down is pushed out by the growing feather Each feather has its origin in a feather germ at the base of the follicle All growth of the feather takes place in its basal portion This causes successive sections to be pushed upward and outward so that in a few days the developing feather germ is visible above the skin This is the pinfeather stage, the

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other breed after 75 hours of incubation. The skin of Rhode Island Red embryos grafted onto White Leghorn embryos developed red down. The skin of embryos having black down grafted onto White Leghorn

Fig 31 A diagrammatic drawing of a body feather from a Leghorn hen. A, shows the complete feather, B, a new feather, C, a detailed enlargement of the barbs and barbules (6) of the web, D, the jointed barb of the fluff. The numerals refer to the following parts 1, quill, 2, shaft, 3 accessory plume 4, fluff, 5 web 6, enlarged barbules connecting barbs, 7, a new feather with soft quill 8 barbs 9, anterior barbule, 10, barbicels (hooklets, hamuli), 11, posterior barbule 12 barbicels on median side, 13, jointed barbule, 14, spikelets (From *International Poultry Guide*, by Payne and Avery, courtesy of International Baby Chick Association)

embryos developed black down. The skin of White Leghorn embryos failed to develop white down when grafted onto embryos having black down or onto Rhode Island Red embryos. The results show that, when skin ectoderm from pigmented breeds is grafted onto unpigmented hosts, black or red pigment develops in accordance with the color of the donor embryo. (If the donor is less than 60 hours of age at grafting

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Fig. 29.—A 6-day-old Barred Plymouth Rock chick with White Wyandotte head

A

B

C

D

E

F

symbol for Venus, the symbol represents the mirror of the goddess
The use of these signs in matings and in certain tables and figures saves
space and is a matter of convenience to readers

Symbols for Color Genes. In the following pages, symbols are used
to designate the various genes that have been determined to be re-
sponsible for the inheritance of certain characters These symbols are
purely arbitrary and are subject to change as more knowledge is gained
concerning the inheritance of characters whose genetics have not pre-
viously been determined

Fig 33 Left to right, sex linked barring in Barred Plymouth Rock autosomal bar
ring in Silver Campine barring in Silver Penciled Hamburg black spangling in
Silver Spangled Hamburg white tipping in Mottled Ancona white spangling in
Speckled Sussex

With a view toward giving the reader a better understanding of the
subsequent discussion on the inheritance of plumage colors and feather
patterns, a brief discussion is presented here concerning symbols used
for genes responsible for the absence or presence of color and for dif-
ferent kinds of feather patterns

Birds with solid white plumage are of two kinds The White Leg-
horn's plumage is due to an autosomal dominant gene that prevents or
inhibits other genes from expressing their effects hence the symbol I
The white plumage of other white varities is due to an autosomal reces-
sive gene c, lack of color, and recessive white varieties also carry i
Solid black plumage is due to the presence of C, for color and an auto-
somal gene E, which extends black pigment to all parts of the plumage,
and, of course, all blacks carry i

In Fig 33 are shown six feathers representing different kinds of black-
and-white patterns within the feather Black-and-white barring in the
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The genes causing crescentric penciling in the feathers of Dark Cornish females and in the females of Silver-Penciled and Partridge (golden-penciled) varieties have not been determined

Columbian plumage, as shown in Fig 39, is due to the combined effects of *e* and the sex-linked gene *S* for silver, the result being a bird with white plumage except for black in the neck, wing, and tail feathers, with some exceptions (see Fig 39, Black-Tailed Japanese Bantams and Lakenfelders)

PLUMAGE COLORS AND PATTERNS

In Chapter 1 it was pointed out that the self-colored or solid-colored breeds and varieties are those with white, black, or blue plumage, the blue having various shades in certain sections   It was also pointed out that apparently all other breeds and varieties have parti-colored plumage, with a wide variety of plumage patterns   The discussion in this chapter deals with the results of research on the genetics of plumage colors and patterns

Dominant White. Bateson (1902) demonstrated that the White Leghorn is white because of the presence of a gene that prevents the production of melanic pigment   This fact was confirmed later by several other workers, some of whom showed that the White Leghorn also has genes for color and barring   These genes are not able to express their effects because of the presence of the inhibiting gene, the symbol for which is *I*   Rhode Island Whites may carry this inhibiting gene, since their ancestry traces back to Rose Comb White Leghorns, White Wyandottes, and Partridge Cochins   Some Pit Games are also said to carry *I*   Some strains of White Minorcas, White Wyandottes, and White Plymouth Rocks have been known to carry *I*, the gene having been introduced by crossing birds of these varieties with White Leghorns

That the dominant inhibiting gene is not always completely dominant to black has been shown by crossing White Leghorns with black varieties   At hatching time a few of the chicks may have a few black flecks, and as adults these birds may have a little black in their plumage   The results of crossing White Leghorns with Rhode Island Reds, Partridge Plymouth Rocks, and Buff Minorcas have shown that *I* is incompletely dominant to red and buff   Most F₁ adult males had red or buff shoulders and some red or buff over the back, and most F₁ adult females varied from having a reddish or buffish cast on the under side of the throat and over the breast to being almost completely red or buff

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Columbian plumage, as shown in Fig 39, is due to the combined effects of *e* and the sex-linked gene *S* for silver, the result being a bird with white plumage except for black in the neck, wing, and tail feathers, with some exceptions (see Fig 39, Black-Tailed Japanese Bantams and Lakenfelders)

PLUMAGE COLORS AND PATTERNS

In Chapter 1 it was pointed out that the self-colored or solid-colored breeds and varieties are those with white, black, or blue plumage, the blue having various shades in certain sections It was also pointed out that apparently all other breeds and varieties have parti-colored plumage, with a wide variety of plumage patterns The discussion in this chapter deals with the results of research on the genetics of plumage colors and patterns

Dominant White. Bateson (1902) demonstrated that the White Leghorn is white because of the presence of a gene that prevents the production of melanic pigment This fact was confirmed later by several other workers, some of whom showed that the White Leghorn also has genes for color and barring These genes are not able to express their effects because of the presence of the inhibiting gene, the symbol for which is *I* Rhode Island Whites may carry this inhibiting gene, since their ancestry traces back to Rose Comb White Leghorns, White Wyandottes, and Partridge Cochins Some Pit Games are also said to carry *I* Some strains of White Minorcas, White Wyandottes, and White Plymouth Rocks have been known to carry *I*, the gene having been introduced by crossing birds of these varieties with White Leghorns

That the dominant inhibiting gene is not always completely dominant to black has been shown by crossing White Leghorns with black varieties At hatching time a few of the chicks may have a few black flecks, and as adults these birds may have a little black in their plumage The results of crossing White Leghorns with Rhode Island Reds Partridge Plymouth Rocks, and Buff Minorcas have shown that *I* is incompletely dominant to red and buff Most F₁ adult males had red or buff shoulders and some red or buff over the back, and most F₁ adult females varied from having a reddish or buffish cast on the underside of the throat and over the breast to being almost completely red or buff

$$\left.\begin{array}{l} 1\ CCoo \\ 2\ Ccoo \end{array}\right\}3 \text{ containing } C \text{ but not } O$$

$$\left.\begin{array}{l} 1\ ccOO \\ 2\ ccOo \end{array}\right\}3 \text{ containing } O \text{ but not } C \left.\phantom{\begin{array}{l}1\\2\\3\end{array}}\right\}7 \text{ white birds}$$

$$1\ ccoo \quad\quad 1 \text{ containing neither } C \text{ nor } O$$

Quinn (1936), however, secured white progeny only from matings of White Silkies × White Rose-Comb Bantams, White Silkies × White Wyandottes, and White Rose-Comb Bantams × White Wyandottes These results suggested that Quinn's White Silkies and Rose-Comb White Bantams were recessive for the same gene Quinn and Godfrey (1937) mated White Silkies with colored birds and secured an F_2 generation of 1748 colored and 606 white chicks, the ratio of colored to white being about 3 1 Backcross matings of White Silkies and F_1 colored birds produced 715 colored and 717 white chicks, almost exactly a 1 1 ratio The F_2 generation secured from an original mating of White Rose Comb Bantams with colored birds consisted of 91 colored and 35 white chicks, approximately a 3 1 ratio Backcross matings of White Rose-Comb Bantams and F_1 colored birds produced 67 colored and 65 white chicks, almost exactly a 1 1 ratio These results confirm those secured by Quinn indicating that their White Silkies and Rose-Comb White Bantams were recessive for the same gene, and Quinn and Godfrey's results also showed that White Wyandottes were recessive for the same gene As an alternative to the Bateson and Punnett (1908) chromogen–oxidase theory, Kimball (1950) suggested that the results they secured were due to a pair of autosomal genes, the recessive allele of either gene in a homozygous condition being responsible for recessive white plumage Dominant-white plumage results from a blockade of the color transfer mechanism

Since birds with the recessive-white plumage carry c, indicating lack of color, any other genes affecting plumage pattern that they may carry cannot be expressed The results of numerous experiments have shown that recessive whites may carry genes for gold, silver, sex-linked barring and numerous other genes These genes are cryptomeres because they cannot produce their effects in the absence of the gene for color

Crossing Recessive and Dominant Whites. Bateson and Punnett (1908), from an original mating of White Wyandottes × White Leghorns, and Hadley (1914), from an original mating of White Plymouth Rocks × White Leghorns, secured F_2 generations consisting of white and colored birds in the ratio of 13 3 How this ratio is obtained is shown in Fig 35, where the inhibiting gene, I, and the gene for color

$$\left.\begin{array}{ll} 1\ CCoo \\ 2\ Ccoo \end{array}\right\} 3 \text{ containing } C \text{ but not } O$$

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Down Color   The down color of the chicks of all black breeds and varieties is black, except that there is usually a variable amount of white or gray on the ventral surface

How Black Behaves in Inheritance   Black is recessive to the white of the White Leghorns but dominant to white in all recessive white breeds and varieties

In a cross between Black Langshans and Brown Leghorns made by Punnett and Bailey, it is reported by Punnett (1923) that the F_1 chicks were black and that as adults the pullets were full black, whereas the cockerels were black with some gold in the hackles and on the shoulders "In the F_2 progeny the black and the brown striped downs segregated cleanly, giving a simple 3 1 ratio" Punnett adds that the results of this cross suggest that brown is differentiated from black by a single gene and that there are various forms of brown which can be transformed into black by the addition of this gene

In black breeds and varieties, the melanic pigment is distributed evenly to all parts of the plumage   From crosses between Black Orpingtons and Light Brahmas, which have black restricted to the neck, wings, and tail, Dunn (1922a, 1923) has suggested that black breeds and varieties contain a pair of genes, designated EE, for the extension of the black or melanic pigment   When blacks are mated with recessive whites, the F_1 progeny, Ee, are black

Occasionally the inheritance of black cannot be interpreted on a monohybrid basis, a case in point being a cross reported by Punnett (1923) between Black Langshans and Golden-Penciled Hamburgs   The F_1 chicks were all black, and as adults the females were solid black and the males were black with some gold in the hackles   The F_2 progeny consisted of 113 blacks and 80 nonblacks, which is very close to a 9 7 ratio (108 56   84 42)   This suggests the inheritance of black in this particular cross on a dihybrid instead of a monohybrid basis   Moreover, F_1 birds backcrossed to Golden-Penciled Hamburgs produced 29 blacks and 92 nonblacks, expectation being one-fourth blacks in the total progeny or a proportion of 30 25 blacks to 90 75 nonblacks   It is quite evident, therefore, that the Golden Penciled Hamburg apparently has two genes affecting the extension of black pigment

Hormones for Testing Genotypes   When certain crosses are made the F_1 results secured have seemed to indicate that sex-linked inheritance was involved, whereas when adequate tests have been applied such has been found not to be the case   Quinn and Burrows (1935) crossed a Black Sumatra male with a White Wyandotte female and observed that the F_1 progeny at hatching time were all black but that at about 4 months of age the F_1 males began to show gold and silver in the hackle

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recessive whites produce equal numbers of blue and black progeny
The same results are obtained when Blue Andalusians are mated to
birds with black plumage   Using the symbol *Bl bl* for blue, *Bl Bl* for
blue-splashed white, and *bl bl* for black, the results indicated for the
following matings should be quite clear

		Progeny	
	Bl -Sp		
Andalusian Matings	White	Blue	Black
Blue × Blue *Bl bl* × *Bl bl*	**1** *Bl Bl*	**2** *Bl bl*	**1** *bl bl*
Blue × Bl Sp *Bl bl* × *Bl Bl*	**1** *Bl Bl*	**1** *Bl bl*	
Blue × Black *Bl bl* × *bl bl*		**1** *Bl bl*	**1** *bl bl*
Crosses			
Bl And × Rec Wh *Bl bl CC* × *bl bl cc*		**1** *Bl bl Cc*	**1** *bl bl Cc*
Bl And × Blacks *Bl bl CC* × *bl bl CC*		**1** *Bl bl CC*	**1** *bl bl CC*

It is interesting to note that the gene *Bl* has a cumulative effect, in a
heterozygous state, pigmentation is partially restricted, whereas, in a
homozygous state, pigmentation is almost completely restricted

True-Breeding Blue. Munro (1946) secured true-breeding blue
chicks in the F_2 generation of an original mating between a black variety
× White Leghorn   He concluded that this new type of blue plumage is
determined by a sex-linked gene that is either an allele of the sex linked
gene for barring or closely linked to it   In their adult plumage females
and males heterozygous for the gene are blue barred   Males homozygous
for the gene are practically pure white

Mottling. The Ancona and Mottled Houdan have black plumage,
except that about every third or fifth feather is tipped with white

Down Color The down color of Ancona chicks is black on the dorsal
surface and creamy yellow shading to white on the lower part of the
head, the breast, and ventral surface   The down color of the Mottled
Houdan chicks is black on the dorsal surface and on the sides of the
body, including the outer thighs, whereas the crest, throat, breast, and
fluff are lemon yellow

Inheritance of Mottling Asmundson and Milne (1930) made crosses
between Mottled Anconas and each of the following colored varieties
Black Minorcas, Black Orpingtons, and Buff Wyandottes   The crosses
between Mottled Anconas and Black Minorcas and Black Orpingtons
produced F_1 birds that were entirely black and F_2 birds consisting of
45 black and 14 mottled ones, the expected ratio on a monohybrid basis
being 44 25 blacks to 14 75 mottled ones   The results of the F_1 and
various backcross matings indicate that mottling is recessive to self-
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Blue × Bl Sp *Bl bl* × *Bl Bl*	1 *Bl Bl*	1 *Bl bl*	
Blue × Black *Bl bl* × *bl bl*		1 *Bl bl*	1 *bl bl*
Crosses			
Bl And × Rec Wh *Bl bl CC* × *bl bl cc*		1 *Bl bl Cc*	1 *bl bl Cc*
Bl And × Blacks *Bl bl CC* × *bl bl CC*		1 *Bl bl CC*	1 *bl bl CC*

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"Red." With the possible exception of the Red Leghorn, there is no solid red breed or variety of chicken From the standpoint of inheritance studies on plumage patterns, geneticists consider Rhode Island Reds, New Hampshires, Red Sussex, and Black-Tailed Red Leghorns as "red" varieties The color is red except for black in the wings and tails of both sexes and in the hackle of the males and frequently in the neck feathers of the females

Warren and Gordon (1933) observed that the density of red in Rhode Island Reds is due to multiple genes, which is to be expected in view of the great variability that normally exists in shades in most Rhode Island Red flocks Hays (1935) crossed exhibition strains of Rhode Island Reds, with relatively dark red plumage, with production-bred strains of the same breed, with relatively light red plumage, and observed that the red plumage of the progeny was of intermediate density, the progeny of the dark red dams being much darker than the progeny of the light red dams Judging by the results secured by Hays, White and Sanborn (1948) with an exhibition strain of Rhode Island Reds, cumulative genes determine the degree of density of red

Identification of Sex at Hatching Time The down color of the chicks of these "red" breeds and varieties varies considerably in the shade of red The lightest chicks are cream-colored, with perhaps but a tinge of red, whereas the darkest chicks are a chocolate brown Frequently the ventral surface is of a lighter shade of red than the dorsal surface, and occasionally dark striping is present

Byerly and Quinn (1936) made the interesting observation that the sex of Rhode Island Red chicks can be distinguished at hatching time with a reasonable degree of accuracy by an examination of the down color Quinn and Byerly (1937) confirmed their original observation with other strains of Rhode Island Red chicks and found that it also applied to New Hampshire chicks Female chicks for the most part had either a black spot at the base of the head or black striping on the head and along the back, or both, whereas male chicks were for the most part free of both spotting and striping Similar observations were made by Hays (1940) This method of "sexing" chicks is probably not sufficiently accurate, however, for poultry breeders or hatchery operators to use for the purpose of selling males and females separately

Hays and Klein (1943) described an improved method of sex identification in Rhode Island Red chicks at hatching time The chicks are held with both wings outstretched, and differences are noted in the areas and degree of pigmentation of the dorsal surface and it is determined whether or not there are black spots on the head Jaap (1946) gave the following brief statement of the method
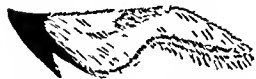
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Males   Females

Fig. 36 Down patterns of day-old New Hampshire chicks show variation in sex dimorphism according to the scheme sketched here. A high correlation was discovered between the down patterns of male chicks and the sex eminence. Males with grades 4 and 5 had the "more masculine" type of sex eminence. Type 1 males and females respectively, are the most easily recognizable winged-sex patterns. (Koem, 1950)

FIG 36 Down patterns of day-old New Hampshire chicks show variation in sex dimorphism according to the scheme sketched here. A high correlation was discovered between the down patterns of male chicks and the sex comb, etc. Males with grades 4 and 5 had the "more masculine" type of sex comb, etc. Type 4 males and females respectively, are the most easily recognizable winged sex patterns (Koom, 1950)

salmon-colored breast feathers of the Light Brown Leghorn female to turn black (see Fig. 37).

Greenwood and Blyth (1929) observed that hyperthyroidism in the Brown Leghorn male gives rise to an increase in the melanic pigment in the feathers while the red pigment tends to disappear. In the female, the effects of hyperthyroidism are slight. It was further shown that when the thyroid was removed there was a diminution in the amount of melanic pigment formed and a coincident increase in the amount of red pigment.

The effects of thiouracil, which inhibits the secretory activity of the thyroid, on pigmentation of the plumage of young Brown Leghorn chickens were studied by Juhn (1946). She found that males tended to assume a reddish color. In females, the feathers on the ventral surface of the body largely retained their normal coloration but the feathers on the dorsal surface became greatly elongated and reddish in color. Juhn (1944) showed that thiouracil administration to Brown Leghorn capons caused the normal black feathers to be replaced by red feathers, which were elongated and had reduced barbulation.

Cream. Taylor (1932a) crossed Black Minorcas × Silver-Spangled Hamburgs and secured a male with typically gold-colored plumage except that his hackle, saddle, and wing-flight feathers were depigmented. This male mated to related gold-colored females produced cream-colored and gold-colored daughters. The following results were secured from three types of matings:

> Heterozygous gold × heterozygous gold produced three golds to one cream. Heterozygous gold × cream produced equal numbers of gold and cream. Cream × cream produced cream-colored progeny only.

It was concluded that the gene for cream is an autosomal diluter of gold.

Punnett (1948) mated a Buff Leghorn male × cream-colored females and secured light gold-colored offspring only. An F_2 generation was secured consisting of 113 golds and 45 creams, approximately three golds to one cream. Some F_2 males and females with the least amount of melanic pigment were mated together and produced an F_3 generation of cream-colored birds with one exception. A mating of a Brown Leghorn male × cream-colored females produced gold-colored progeny with nondescript melanic markings that were more pronounced in females than in males. F_1 males and females mated among themselves produced an F_2 progeny consisting of 172 golds and 53 creams, approximately 3 : 1. Subsequent matings led to the establishment of a strain

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Punnett (1923) reported the results of crosses between various black varieties and Buff Cochins, Brown Leghorns, and Golden-Penciled Hamburgs In every cross the adult plumage of the F_1 females was solid black and the adult plumage of the F_1 males was black with gold in the hackles and sometimes on the shoulders
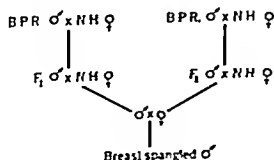
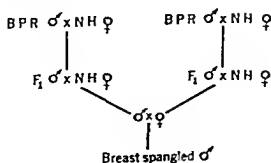Dunn (1923) concluded that buff differs from black by a gene determining the restriction of black to the hackle, wings, and tail As pointed out under the discussion of the inheritance of black, solid black is due to the extension gene E The buff pattern is due to gene e, which in a homozygous condition restricts black to the neck, tail, and wing feathers

Knox (1927) concluded that two pairs of genes with cumulative effects differentiate buff plumage from solid-black plumage The results that Knox secured in his F_2 and backcross generations led him to make the following assumptions Buff is epistatic to black when three or four genes for buff are in the presence of CC and EE, buff is epistatic to black when three or four genes for buff are in the presence of either Cc and EE or CC and Ee, buff is epistatic to black when two or more genes for buff are in the presence of Cc and Ee

Spanglng. Spanglng is found in Silver-Spangled and Golden-Spangled Hamburgs, in which the spangle at the tips of the feathers is black, and in Speckled Sussex, Old English Spangled Games, and Mille Fleur bantams, in which the spangle at the tips of the feathers is white

So far as is known, no research has been conducted on the inheritance of white spangling in the latter three breeds mentioned The inheritance of black spangling in the Hamburgs has been reported upon by Punnett (1923), Lefevre and Rucker (1923), and Taylor (1932b, 1933) Although Lefevre and Rucker concluded that black spangling was sex-linked, this theory was disproved by Taylor, who concluded, from the results secured by crossing Black Minorcas and Silver-Spangled Hamburgs, that spangling is due to a dominant autosomal gene, Sp

It is interesting to note that Juhn and Hess (1947) observed spangled breast feathers in the adult plumage of a male secured from the matings listed below, the original matings consisting of Barred Plymouth Rock males × New Hampshire females

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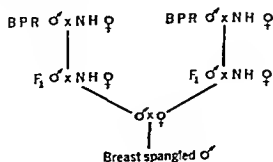
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Spangling.

Spangling is found in Silver-Spangled and Golden-Spangled Hamburgs, in which the spangle at the tips of the feathers is black, and in Speckled Sussex, Old English Spangled Games, and Mille Fleur bantams, in which the spangle at the tips of the feathers is white

So far as is known, no research has been conducted on the inheritance of white spangling in the latter three breeds mentioned The inheritance of black spangling in the Hamburgs has been reported upon by Punnett (1923), Lefevre and Rucker (1923), and Taylor (1932b, 1933) Although Lefevre and Rucker concluded that black spangling was sex-linked, this theory was disproved by Taylor, who concluded, from the results secured by crossing Black Minorcas and Silver-Spangled Hamburgs, that spangling is due to a dominant autosomal gene, Sp

It is interesting to note that Juhn and Hess (1947) observed spangled breast feathers in the adult plumage of a male secured from the matings listed below, the original matings consisting of Barred Plymouth Rock males × New Hampshire females

BPR ♂ × NH ♀   BPR ♂ × NH ♀

F_1 ♂ × NH ♀ F_1 ♂ × NH ♀

♂ × ♀

Breast spangled ♂

Punnett (1923) reported the results of crosses between various black varieties and Buff Cochins, Brown Leghorns, and Golden-Penciled Hamburgs   In every cross the adult plumage of the F_1 females was solid black and the adult plumage of the F_1 males was black with gold in the hackles and sometimes on the shoulders

Dunn (1923) concluded that buff differs from black by a gene determining the restriction of black to the hackle, wings, and tail   As pointed out under the discussion of the inheritance of black, solid black is due to the extension gene E The buff pattern is due to gene e, which in a homozygous condition restricts black to the neck, tail, and wing feathers

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from the rest of the feather In Fig 34 are shown the penciled feathers of a Dark Cornish female, Partridge Cochin female, and Silver-Penciled Plymouth Rock female The tail feathers of penciled females are black None of the feathers of the males of any of the penciled varieties is penciled, as shown in Fig 6 Up to the present, practically nothing is known concerning the genetics of penciling

Autosomal Barring. Among the Campines, an interesting situation exists regarding three different kinds of barring The Silver variety has black and white bars, the Golden variety black and golden-bay bars, and the Chamois variety white and golden-bay bars

Since the plumage of the Silver variety is dominant to that of the Golden variety, Punnett (1923) pointed out that the white bars of the Silver variety are due to the action of a gene which inhibits the development of golden bay Punnett further pointed out that the plumage of the Chamois is dominant to the plumage of the Golden variety, the difference between white and golden-bay bars and black and golden-bay bars being due to a single gene, *ab*, suggested by Hutt (1949)

It is apparent, then, that the golden-bay bars of the Chamois variety correspond to the golden-bay bars of the Golden variety, and that the Chamois variety contains a gene which inhibits the development of the melanic pigment contained in the black bars of the Golden variety Therefore, a cross between the Silver and Chamois varieties should produce white birds, which Punnett found to be the case

It is interesting to observe that the neck feathers, except those in front, of Silver Campines and Golden Campines are free of barring, indicating the presence of a modifying gene involved in the distribution of black

Nickerson (1946*b*) showed that castration of Silver Campine males at about 2 months of age resulted in the deposition of red pigment in the regenerating feathers It was further found that injection of adequate doses of either male or female sex hormone into the capons brought about a return of black pigmentation

Autosomal barring also occurs in Golden-Penciled and Silver-Penciled Hamburgs (see Fig 4) In the females of these two varieties so-called penciling consists of narrow parallel bars of greenish black across most feathers over the body In the males of these two varieties black is restricted to the wings, tail, and a few of the body and fluff feathers barring occurring in some of the wing and body and fluff feathers Penciled Hamburgs, therefore, present an unusual situation, since the females appear to carry *L*, whereas the males appear to carry *ee*, perhaps with modifiers

Columbian. The Delawares breed and these five varieties have the "columbian" pattern of plumage Columbian Leghorns Columbian

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from the rest of the feather. In Fig 34 are shown the penciled feathers of a Dark Cornish female, Partridge Cochin female, and Silver-Penciled Plymouth Rock female. The tail feathers of penciled females are black. None of the feathers of the males of any of the penciled varieties is penciled, as shown in Fig 6. Up to the present, practically nothing is known concerning the genetics of penciling.

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It is interesting to observe that the neck feathers, except those in front, of Silver Campines and Golden Campines are free of barring, indicating the presence of a modifying gene involved in the distribution of black.

Nickerson (1946b) showed that castration of Silver Campine males at about 2 months of age resulted in the deposition of red pigment in the regenerating feathers. It was further found that injection of adequate doses of either male or female sex hormone into the capons brought about a return of black pigmentation.

Autosomal barring also occurs in Golden-Penciled and Silver-Penciled Hamburgs (see Fig 4). In the females of these two varieties, so-called penciling consists of narrow parallel bars of greenish black across most feathers over the body. In the males of these two varieties black is restricted to the wings, tail, and a few of the body and fluff feathers barring occurring in some of the wing and body and fluff feathers. Penciled Hamburgs, therefore, present an unusual situation, since the females appear to carry *E*, whereas the males appear to carry *ee*, perhaps with modifiers.

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from the rest of the feather   In Fig 34 are shown the penciled feathers of a Dark Cornish female, Partridge Cochin female, and Silver-Penciled Plymouth Rock female   The tail feathers of penciled females are black None of the feathers of the males of any of the penciled varieties is penciled, as shown in Fig 6   Up to the present, practically nothing is known concerning the genetics of penciling

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Columbian.   The Delawares breed and these five varieties have the "columbian" pattern of plumage   Columbian Leghorns, Columbian

Plymouth Rocks, Columbian Wyandottes, Light Brahmas, and Light Sussex   The plumage in both sexes is white, except that the neck feathers of the female, the hackle feathers of the male, and the wings and tail of both sexes contain black   The neck and hackle feathers, the tail coverts of the female, and the saddle and sickle coverts of the male are black laced with white   In addition, in the Light Brahma the feathers on the shanks and toes are black laced with white   The Delawares breed has columbian plumage pattern with white barring in the feathers showing black   The Black-Tailed Japanese Bantam has a modified columbian plumage pattern, inasmuch as there is black in the large wing feathers and the tail feathers but the neck feathers are white   In Lakenfelders, however, the neck, tail, and large wing feathers in both sexes are solid black, and the male saddle and sickle feathers are also solid black

Sturtevant (1912) and Dunn (1923) observed that the columbian pattern of the Light Brahma and other columbian-colored varieties is due to the presence of the dominant sex-linked gene S, for "silver," and a non-sex-linked gene e, which restricts the black to the neck, wings, and tail   Light Brahma and similar males, being homozygous for silver, transmit it to their daughters and sons, whereas Light Brahma and other columbian-colored females, being heterozygous for silver, transmit it to their sons only   In addition, Dunn has suggested that there are multiple genes determining the amount of black pigment developed in the feathers of the neck, wings, and tail (see Fig 39)

A mating of a New Hampshire male × females with columbian plumage pattern produces F_1 male progeny with columbian plumage pattern and F_1 females that are mostly buff (gold) to red in color, as shown herewith

New Hampshire × Columbian

P_1 zygotes	$eess$	$eeS-$
P_1 gametes	es	eS and $e-$
F_1 zygotes	$eeSs$	$ees-$
	columbian males	buff or red females

New Hampshires, Rhode Island Reds, and all buff varieties carry ee but of course lack the gene for silver

Sex-Linked "Silver." The terms silver and gold are used with reference to two well-known ground colors of the down of chicks of several different breeds and varieties   With respect to adult plumage, Silver-Penciled Wyandottes and Partridge Plymouth Rocks (see Fig 6) are representative of the respective color classes

To the "silver" class belong the Silver-Laced and Silver-Penciled Wyandottes, Silver Campines, Silver-Penciled Plymouth Rocks, Silver-

Plymouth Rocks, Columbian Wyandottes, Light Brahmas, and Light Sussex The plumage in both sexes is white, except that the neck feathers of the female, the hackle feathers of the male, and the wings and tail of both sexes contain black The neck and hackle feathers, the tail coverts of the female, and the saddle and sickle coverts of the male are black laced with white In addition, in the Light Brahma the feathers on the shanks and toes are black laced with white The Delawares breed has columbian plumage pattern with white barring in the feathers showing black The Black-Tailed Japanese Bantam has a modified columbian plumage pattern, inasmuch as there is black in the large wing feathers and the tail feathers but the neck feathers are white In Lakenfelders, however, the neck, tail, and large wing feathers in both sexes are solid black, and the male saddle and sickle feathers are also solid black

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P_1 gametes	es	eS and $e-$
F_1 zygotes	$eeSs$	$ees-$
	columbian males	buff or red females

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The barred female being hemizygous for sex transmits the B gene to her sons only, the barred male being homozygous for sex transmits the B gene to his daughters as well as to his sons

Identifying Sex at Hatching Time   The down color of Barred Plymouth Rock chicks is black over the dorsal surface and on the sides, except that there is a light yellowish gray patch at the back of the head, and the ventral surface is creamy white, the extent of this color varying considerably

Jerome (1939) was able to distinguish the sex of production-bred Barred Plymouth Rock chicks with a relatively high degree of accuracy

Fig 40   Showing differences in types of head spots in male and female Barred Plymouth Rock chicks males above and females below (Jerome 1939)

by the differences between the sexes in head spots and shank coloring One of the chief differences noted with respect to head spotting was that in females the head spot was usually more regular in outline and was pointed anteriorly (see Fig 40)   Shank color is usually lighter in males than in females   The important difference between the sexes with respect to shank color is that in males the shanks and feet are an even blend whereas in females the darker shank color terminates rather abruptly at the base of the shank, the toes being lighter in color

Gerry and Mishler (1949), using the above method, were able to sex commercial lots of chicks secured from different hatcheries with an accuracy of 90 per cent   In order to sex the other 10 per cent more accurately, they developed more refined methods with respect to minor differences in head spot markings

The identification of the sex of crossbred chicks secured from such matings as Rhode Island Red or New Hampshire males × Barred Plymouth Rock females is relatively simple   The crossbred male chicks have head-spot markings and bright yellow shanks very similar to

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duce zygote *cc Bb Ss*, which would be white at hatching time and would develop into an adult male with barred columbian pattern

Barred columbian patterned females could be secured from a mating of an *Lc Bb Ss* male (from a mating of Barred Plymouth Rock male × New Hampshire female or the reciprocal mating) and an *Lc B– S–* female The *cBS* gamete of male origin and the *c– –* gamete of female origin would produce an *cc B– S–* zygote, which would develop into a female with barred columbian pattern

Autosexing Breeds. The demand on the part of many market-egg producers for pullet chicks exclusively led to the development of several autosexing breeds In these breeds the sexes can be identified at hatching time with a high degree of accuracy

Apparently the first autosexing breed was the Golden Cambar, developed in England by Punnett and Pease (1930) This breed was developed by crossing Golden Campines and Barred Plymouth Rocks and for two or three successive generations backcrossing the barred cockerels to Golden Campine females At hatching time, Cambar males have pale "blotchy" down whereas Cambar females have down color characteristic of the Golden Campine chicks

Other autosexing breeds include Legbars developed by Punnett (1942) from an original cross between a Brown Leghorn male × Barred Plymouth Rock female, Oklabars by Jaap (1941) from matings involving Rhode Island Reds, White Plymouth Rocks, and Dark Cornish, Ancobars by Lamoreux (1941) from crossing Anconas with Barred Plymouth Rocks, Buffbars, Brussbars, and Dorbars by Pease (1941) from Buff Orpingtons, Brown Sussex, and Silver-Gray Dorkings respectively, crossed with Barred Plymouth Rocks, Silver Cambars and Cream Legbars described by Pease (1948), and Redbars described by Hill and Lloyd (1950)

The future of autosexing breeds will undoubtedly depend largely upon the extent to which high laying ability becomes one of their outstanding characteristics In England, autosexing breeds appear to be gaining in popularity

Loss of Pigmentation. Several cases have been reported of colored females' turning completely or almost completely white Only a few need be mentioned Lippincott (1920) described a Blue Andalusian that gradually became completely white but produced normal bluecolored chicks when mated to a Blue Andalusian male Crew (1922) reported the case of a Black Leghorn that became white within a year Godbey and Reid (1931) stated that a Barred Plymouth Rock that had turned almost completely white produced colored chicks when mated to a White Plymouth Rock male

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brown, and black iris, melanin or black pigment is present, as well as the other two

Warren and Gordon (1933) were not able to determine that variations in iris color in Rhode Island Reds are inherited Slinger and MacIlraith (1944), from an examination of many birds in several different flocks of Barred Plymouth Rocks, observed a relationship between "green-gray" iris and the number of solid-black feathers Apparently the condition was hereditary rather than pathological in nature

Earlobe Color. Apparently all breeds having white earlobes lay white-shelled eggs, and apparently all breeds except four, having red earlobes lay brown-shelled eggs The Araucana lays a blue-shelled egg, and the Dorkings, Redcaps, and Crevecoeurs lay white-shelled eggs Warren (1928) found that the inheritance of earlobe color is very complex, multiple genes being involved Hays (1943) suggested that mottled earlobes in the strain of Rhode Island Reds he studied were due to two recessive autosomal genes

Yellow Head. Among Barred Plymouth Rock chickens a few weeks old, Deakin and Robertson (1935) observed some with yellow comb, face, and wattles Yellow heads persisted in males until the approach of sexual maturity and then turned orange colored In females, the yellow faded out later than in males, and during egg laying the female heads became pale pinkish This yellow-head condition was found to be due to an autosomal recessive gene, to which Hutt (1949) assigned the symbol *g*

Skin Color. Yellow skin is characteristic of most American breeds, white skin is characteristic of several British and some other European breeds, and the Silkie has dark blue-colored skin

The results of several crosses between varieties having yellow skin and varieties having white skin have been consistent in demonstrating that the gene for white skin is dominant to the gene for yellow skin Dunn (1925) demonstrated that the genes involved are autosomal and assigned the symbols *W* for white skin and *w* for yellow skin *W* does not prevent the storage of carotinoid by birds having white skin, the pigment being stored in the blood and body fat but not in the skin

In varieties that have black plumage and dark slate or black shanks, as in Jersey Black Giants and Black Orpingtons, it is sometimes difficult to tell whether they are yellow-skinned or white skinned According to the American Standard of Perfection, the soles of the feet of Jersey Black Giants are yellow, whereas those of the Black Orpingtons are pinkish white The genes responsible for the dark blue skin of the Silkie have not been determined The pigment is distributed in varying density throughout the connective tissue, periost of the bones, and

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Warren and Gordon (1933) were not able to determine that variations in iris color in Rhode Island Reds are inherited   Slinger and MacIlraith (1944), from an examination of many birds in several different flocks of Barred Plymouth Rocks, observed a relationship between "green-gray" iris and the number of solid-black feathers   Apparently the condition was hereditary rather than pathological in nature

Earlobe Color.   Apparently all breeds having white earlobes lay white-shelled eggs, and apparently all breeds except four, having red earlobes lay brown-shelled eggs   The Araucana lays a blue-red egg, and the Dorkings, Redcaps, and Crevecoeurs lay white-shelled eggs   Warren (1928) found that the inheritance of earlobe color is very complex, multiple genes being involved   Hays (1943) suggested that mottled earlobes in the strain of Rhode Island Reds he studied were due to two recessive autosomal genes

Yellow Head.   Among Barred Plymouth Rock chickens a few weeks old, Deakin and Robertson (1935) observed some with yellow comb, face, and wattles   Yellow heads persisted in males until the approach of sexual maturity and then turned orange colored   In females, the yellow faded out later than in males, and during egg laying the female heads became pale pinkish   This yellow-head condition was found to be due to an autosomal recessive gene, to which Hutt (1949) assigned the symbol g

Skin Color.   Yellow skin is characteristic of most American breeds, white skin is characteristic of several British and some other European breeds, and the Silkie has dark blue-colored skin

The results of several crosses between varieties having yellow skin and varieties having white skin have been consistent in demonstrating that the gene for white skin is dominant to the gene for yellow skin   Dunn (1925) demonstrated that the genes involved are autosomal and assigned the symbols W for white skin and w for yellow skin W does not prevent the storage of carotinoid by birds having white skin, the pigment being stored in the blood and body fat but not in the skin

In varieties that have black plumage and dark slate or black shanks, as in Jersey Black Giants and Black Orpingtons, it is sometimes difficult to tell whether they are yellow-skinned or white skinned   According to the American Standard of Perfection, the soles of the feet of Jersey Black Giants are yellow, whereas those of the Black Orpingtons are pinkish white   The genes responsible for the dark blue skin of the Silkie have not been determined   The pigment is distributed in varying density throughout the connective tissue, periost of the bones, and

simplest manner of presenting the material on shank color is the preceding tabular form, adapted from Hutt (1949), with slight modifications

Since some White Plymouth Rocks have green shanks, as pointed out by Jaap (1943) and Jeffrey (1947), it is interesting to recall Jeffrey's suggestion concerning the difficulty of eliminating this undesirable character so long as the birds carry B and E

Summary. At the conclusion of this chapter on skin and plumage color characters, it seems appropriate to present in Table 2 a list of the dominant and recessive characters

TABLE 2

DOMINANT AND RECESSIVE COLOR CHARACTERS

Character	Dominant or Recessive	Autosomal or Sex Linked
White plumage	In White Leghorns more completely dominant to black than to red	Autosomal
White plumage	In White Minorcas White Plymouth Rocks, etc recessive to color	Autosomal
Albinism	Recessive to normal	Autosomal
Imperfect albinism	Recessive to normal	Sex linked
Black plumage	Dominant to recessive white	Autosomal
Blue plumage	Due to heterozygous condition of color genes	Autosomal
Cream plumage	Dilutes gold	Autosomal
Red plumage	Recessive to black	Autosomal
Buff plumage	Dominant to recessive white, recessive to black	Autosomal
Mottled plumage	Recessive to black	Autosomal
Pied plumage	Recessive to black	Autosomal
Black spangling	Dominant to solid color	Sex linked
Barred plumage	In Plymouth Rocks dominant to nonbarring	Autosomal
Barred plumage	In Campines and Penciled Hamburgs	Sex linked
Silver plumage	Dominant to red buff etc	Autosomal
White skin	Dominant to yellow skin	

PROBLEMS

1 Draw an illustration showing the structure of a feather and name the different parts

2 What is the source of pigment in feathers and how do colored feathers acquire pigmentation?

3 Explain how a ratio of thirteen white to three colored birds is obtained in the F_2 generation secured from an original mating between White Leghorns and White Wyandottes

4 If a Rhode Island Red male is crossed with a Barred Plymouth Rock female and one of the F_1 crossbred females is mated with her sire, with respect to barring

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Frizzled Plumage. The frizzled plumage character is peculiar to the breed known as Frizzles, the feathers of which curl upwards and forwards because of the absence or modification of the hooklets of each feather, a thickening of its barbules and barbs, and alterations in the direction of the barbules and barbs. The plumage has the appearance of being rubbed the wrong way (see Fig 41).

That the frizzled condition of plumage in the domestic fowl has persisted for a long time is borne out by the fact that a frizzled fowl was described by Aldrovandus (1600). From early times frizzled fowls have been reported in many parts of the world.

The genetics of the frizzled plumage character was studied by Crew (1925), Hutt (1930), and Landauer and Dunn (1930a), all of whom showed that the frizzled character was dominant over nonfrizzling. Crew was led to believe that the frizzled character acts as a lethal in a homozygous condition, but Hutt and Landauer and Dunn have shown this not to be the case.

In certain matings Hutt determined that he had secured two kinds of frizzled birds, one group with "ordinary" frizzling and one group with "extreme" frizzling. Five females with ordinary frizzling were mated to a White Leghorn male and produced 33 birds with ordinary frizzling and 29 with normal plumage. Five females with extreme frizzling were mated to the same White Leghorn male and produced 48 birds, all of them having ordinary frizzling. The five females with ordinary frizzling were heterozygous, and the five females with extreme frizzling were homozygous, for the frizzling character.

Landauer and Dunn (1930a) secured results that confirm the observations of Hutt (1930), although they made a distinction between what they call two types of heterozygous frizzling. One type they call "exhibition type" heterozygous frizzling and the other "ordinary-type" heterozygous frizzling, the difference between the two being due to the more conspicuous structural changes in the feathers of the exhibition-type birds. Landauer and Dunn observed that the exhibition type of heterozygous frizzling is the kind which private breeders exhibit at poultry fairs and that it "has been produced by selection and that it depends in its expression upon the presence of other genes beside the gene for frizzling."

The difference between frizzling and nonfrizzling is due to an autosomal gene, *F*, frizzling being incompletely dominant. The homozygous type of frizzling is more extreme than the heterozygous type. Hutt (1932, 1936) and Landauer (1933) have reported the existence of a recessive gene, *mf*, that modifies frizzling, this modifier apparently being widely distributed among various breeds. Birds that are homo-

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zygous for frizzling and homozygous for the modifier lack the extreme curliness of the feathers which characterizes homozygous frizzles that do not have the modifier. Birds that are heterozygous for frizzling and homozygous for the modifier, although showing typical frizzled feathering in the definitive feather stage, resemble normal-plumaged birds as adults.

Frayed Feathering. Warren (1938) reported on the inheritance of a variation in feather structure termed "fray," a condition not recognizable at hatching time. In the wing and tail feathers of the adult, however, there is a defective condition of the barbules, resulting in an imperfect locking of the anterior and posterior barbules (see Fig. 41). The separated barbs give the frayed appearance of the vanes of the feathers. The condition is due to an autosomal recessive gene, designated *fr.*

Flightlessness. A peculiar condition that causes the flight feathers of the wing and some of the other large feathers to break off, as shown in Fig. 41, when subjected to slight pressure has been described by Warren (1932). New feathers that follow the molt also break off as soon as they are sufficiently mature to become dry. Only the base of the shaft and the quill of the flight feathers remain. Marlow and Caldwell (1934) have demonstrated certain chemical and structural differences between "flightless" and normal feathers: Normal feathers contained 22.7 per cent more cystine sulfur but less than one-half as much phosphorus as "flightless" feathers, and X-ray analyses showed the "flightless" feathers to be of abnormal structure.

A heterozygous "flightless" male when crossed with normal females produced progeny one-half of which were flightless and one-half normal, indicating that "flightlessness" is due to an autosomal dominant gene, *Fl.*

Warren (1937a), on the basis of further matings of his "flightless" birds, observed that in a homozygous condition the flightless gene gives rise to birds which appear normal at hatching time but that, at about 4 weeks, retardation of feather growth appeared, with the result that as adults the birds were almost nude of feathers and the beak and toenails were quite fragile. Flightless birds mated to flightless birds produced progeny consisting of 116 flightless, 51 normals, and 16 featherless. Backcross matings of flightless to normal feathering gave approximately a 1 : 1 ratio, indicating that the flightless condition is heterozygous. Apparently the flightless gene in homozygous condition is usually lethal, approximately two-thirds of the homozygous individuals dying, as indicated by the proportion of 116 : 51 : 16 indicated above

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KEY TO LETTERING OF FIGURES

A T	Alar tract	L N S	Lateral neck space
A S T	Anterior spinal tract	I T	Lateral tract
Ca T	Caudal tract	L T S	Lateral trunk space
Cr S	Crural space	I W S	Lower wing space
Cr T	Crural tract	O G	Oil gland
F T	Femoral or lumbar tract	P S T	Posterior spinal tract
H T	Head tract	U W S	Upper wing space
Hu T	Humeral tract	V T	Ventral tract
I S	Inferior space		

FIG 12 The feather tracts on the ventral side A and the dorsal side C of the normal fowl and the feather tracts on the ventral side B and the dorsal side D of the Naked Neck fowl (Greenwood)

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I S	Inferior space		

FIG. 12. The feather tracts on the ventral A and on the dorsal C of the normal fowl and the feather tracts on the ventral B and on the dorsal D of the Naked Neck fowl (Greenwood)

FIG 44 A apterylosis (Sturkie 1942) B a long tailed bird (Kinugawa 1930
C 'stringy feathering (Bu. Bohren and Warren 1950 D vulture hock U S
Dept Agr) E a Naked Neck bird (U S Dept Agr

FIG 44 A apterylosis (Sturkie 1942) B a long tailed bird (Kinugawa 1930 C 'stringy feathering (Bu Bohren and Warren 1950 D vulture hock U S Dept Agr) E a Naked Neck bird (U S Dept Agr

The feather tracts, or pterylae, and the apteria, or relatively bare spaces between the feather tracts, of normal and naked-neck birds are shown in Fig. 42. In normal birds there are some down feathers and semiplumes in the apteria, but in the Naked-Neck fowl the apteria in all regions of the body are bare, as pointed out by Greenwood (1927).

Davenport (1914) and Warren (1933a) demonstrated that the naked-neck character is due to a single dominant autosomal gene, designated *Na* by Hutt (1949).

"Long Tail." The Phoenix and Yokohama fowls, originally of Japan, have extraordinarily long sickle feathers and saddle coverts, sometimes up to 12 to 20 feet, and tail feathers up to 8 feet long (see Fig. 44). According to the rather meager observations of Davenport (1906) and Bonhote (1914), multiple genes are involved.

Vulture Hocks. Two standard American breeds of chicken, the Sultan and the Mille Fleur Booted Bantam have long, stiff feathers that arise from the posterior area of the tibial feather tract, above the tibiometatarsal (hock) joint (see Fig. 44). Davenport (1906) and Jull and Quinn (1931) observed that the vulture hock condition is due to a recessive autosomal gene, designated *v* by Hutt (1949).

Feathered "Shanks." Although in poultry parlance Asiatic breeds, as well as some European breeds and the Silkies, are called feathered-shank breeds, in reality the feathers involved arise from the outside of the tarsometatarsus and appear also on the toes, especially the outer toe of each foot. The term feathered "shanks" has become so well established, however, that there should be no particular objection to retaining it so long as the place of origin of the feathers is kept in mind

The results of early studies on the inheritance of shank feathering were inconclusive. This is understandable when it is realized that breeds differ in degree of shank feathering, that Croad Langshans in England have less profuse shank feathering than standardbred Langshans, and that Cochins have more profuse shank feathering than standardbred Langshans.

Punnett and Bailey (1918) crossed Croad Langshans with Hamburgs and with Brown Leghorns and concluded that shank feathering is dominant to its absence, an autosomal gene being involved. On the other hand, Punnett and Bailey concluded that two autosomal genes are responsible for shank feathering in those breeds having more profuse shank feathering than their Croad Langshans.

Further work by Dunn and Jull (1927), Lambert and Knox (1929), and Hays (1943) has not helped much in solving this very complex problem. At present it is not possible to suggest the number of genes responsible for shank feathering

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muffs and beard are always associated together, in Houdans the beard is larger than the muffs but in most other cases the muffs are larger than the beard. Muffs and beard are due to an incompletely dominant autosomal gene, designated *Mb* by Hutt (1949)

Short Down. Hutt (1951), from matings of Rhode Island Red males × Barred Plymouth Rock females, observed a significant deficiency of female chicks at hatching time and an excess of females among the embryos that died during the latter part of the incubation period These dead female embryos had "clubbed" short down The females that hatched were solid black in down color, and the down was shorter than in male chicks, which had black down except for a white or whitish spot on the top of the head, due to the gene *B* for barring The females also had areas on the dorsal surface where the down was absent or sparse Hutt attributed the shortness and sparseness of down in female embryos and hatched chicks to the pleiotropic (manifold) effects of the gene *B*, which had a semilethal effect on female embryos

Early, Late, and Slow Feathering. Throughout the lifetime of a chicken several changes in plumage take place, the down at hatching time being superseded by chick feathering, which is followed by juvenile plumage, which in turn is followed by adult plumage Chick feathering replaces the down gradually, and subsequent feather changes result from the replacement of feathers in a fairly regular sequence

Appearance of Chick Feathering It has already been pointed out and illustrated in Fig 42 that feathers arise from feather tracts or pterylae The problem of chief concern at this time is to point out the importance of the difference in the rate of the development of wing and tail feathers which often exists between breeds and strains The primaries and secondaries of the wing are called "remiges," and the tail feathers are called "rectrices "

The order in which feathers appear in the feather tracts has been studied by Landauer and Dunn (1930c), Gericke and Platt (1932), Chu (1938), and Radi and Warren (1938) Although there is considerable overlapping with respect to the time that feathers appear in different feather tracts, the order of feather appearance is about as given by Radi and Warren shoulder, thigh, breast, neck, tail, back, wing, leg, abdomen, and head The sequence of feather appearance within feather tracts has been studied by Holmes (1935), Warren and Gordon (1935), and Juhn (1938)

Sequence of Plumages Juvenile plumage succeeds the definitive feathering stage gradually, juvenile feathers making their first appearance in the marginal areas of the feather tracts With respect to the rate of wing and tail feathering, it has long been known that most Leg-

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feathering cockerels and late-feathering pullets The sex-linked nature of late feathering was determined on the basis of tail feather development at 10 days of age (see Fig 45) The symbol for the dominant sex-linked gene for late feathering is *K*

Darrow and Warren (1944) observed that an autosomal dominant gene improves feathering in the presence of *K*

Number of Secondaries at Hatching Time Warren (1925, 1944a) demonstrated that early feathering could be identified in chicks at

Fig 46 Left, wing of late feathering New Hampshire chick at hatching time note that the primaries are poorly developed and no secondaries are visible Right wing of an early-feathering New Hampshire chick at hatching time note the well developed primaries and primary coverts and six well developed secondaries (Glazener and Jull, Univ of Maryland)

hatching time by the length of their primary feathers and the relative length of their coverts, which grow along each primary feather Not only are the primary feathers well developed in early feathering chicks, but also the coverts are about two thirds as long as the primary feathers, whereas in late-feathering chicks the coverts are about as long as the primary feathers, which are almost as slender as the coverts

Darrow (1941) and Darrow and Warren (1944) observed that the number of well-developed secondaries at hatching time was positively correlated with the degree of tail feathering at 10 days of age and with the degree of feathering at broiler age Glazener and Jull (1946), working with Barred Plymouth Rocks and New Hampshires, found that chicks with at least six secondaries at hatching time were heavier at 10 weeks of age than chicks with five or less secondaries (see Fig 46) In order to get a good view of the secondaries in newly hatched chicks the wings should be looked at from the underside

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AT 10 DAYS OF AOE

Normal early feathering at least six primaries and six secondaries equal in length and a well developed tail

Retarded three or four primaries and secondaries of equal length, the successive primary and secondary feathers being progressively shorter, and no tail

Tardy a normal number of primaries but narrower and shorter than in normal early feathering chicks but little or no development of secondaries and no tail

AT 3 WEEKS

Normal early feathering many body feathers, at least eight well developed primaries and secondaries and a prominent tail

Retarded few body feathers, only six primaries and six or more secondaries, and poorly developed tail

Tardy poor feathering over the body, secondaries shorter than the primaries, and no tail

Improving Early Feathering If there is need of improving feathering in White Leghorns, poultry breeders should adopt a breeding and selection program involving the identification and elimination of retarded-feathering chickens at 10 days of age and the identification and elimination of tardy-feathering chicks before they are 8 weeks old At the same time, it is possible that the rejection, for future breeding purposes, of all chicks at hatching time that have less than six secondaries would be equally effective and would involve much less labor

Improving feathering in late-feathering strains can be readily accomplished by introducing k into the flock This has already been done in several strains of Barred Plymouth Rocks, White Plymouth Rocks New Hampshires, and Rhode Island Reds On the other hand, some late-feathering strains have been shown to have a few birds carrying l, in which case it is a fairly simple matter to change the strain into an early-feathering one Future breeding stock should be selected at hatching time from among the chicks with at least six secondaries

Slow Feathering Late feathering in some general-purpose breeds may be so variable that at about 6 to 12 weeks of age some of the chickens are known as "barebacks" (see Fig 48) This slow-feathering condition is due to autosomal genes Occasionally a few White Leghorn chickens in certain strains may also be afflicted with this bareback condition "Barebacks" are a menace to broiler growers

Hen Feathering in Males Among the various breeds of chickens, the Campines (see Fig 4) and the Sebright Bantams are known as "hen-feathered" breeds, inasmuch as in these breeds the male hackle and saddle feathers are of the same shape, color, and relatively the same length as in the female

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The results of several crosses made by different investigators showed that hen feathering is dominant to cock feathering, the symbol *Hf* being designated by Hutt (1949) for the gene that causes hen feathering. Punnett (1937) suggested that hen feathering is caused by a single dominant autosomal gene, the effects of which are possible only when the gene is activated by testicular hormone. Haldane (1942) suggested

Fig. 49 Effect of sex hormones on plumage type of males of the Silver Sebright Bantam, a hen-feathered breed. Left, a normal saddle feather. Second from left, a capon saddle feather, castration results in the development of male-type feathering Third from left, a saddle feather from a capon treated with male sex hormone Right, saddle feather of a capon treated with female sex hormone. (Selye, 1947)

that the gene for hen feathering renders the feather-producing cells sensitive to most of the male sex hormones in their physiological reactions. He stated that in all probability hen feathering in males is due to the testosterone secreted by the testes and not to any traces of estrogens which they may secrete and that the gene must act on the feather-producing tissues and not on the gonads.

Selye (1947) demonstrated that castration of a Silver Sebright male resulted in the capon's acquiring typical cock feathering. When the capon was treated with female sex hormone, the subsequent plumage was henny (see Fig. 49).

Greenwood and Blyth (1940-1941) described an inbred Brown Leghorn cock that acquired female plumage during its first adult molt but a year later reverted to male feathering Subsequent reversal from

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Comb Type. Among the various domestic breeds of chickens, the type of comb is usually a breed or variety characteristic For instance, all Plymouth Rocks have single combs, all Wyandottes have rose combs, but there are single-comb Rhode Island Reds and rose-comb Rhode Island Reds, as well as single-comb and rose-comb White Leghorns There are, however, variations within single and rose combs The Leghorn single comb is supposed to have five points or serrations, whereas the Minorca single comb is supposed to have six points, the spike at the rear of the Wyandotte rose comb turns downward, whereas the longer spike of the Hamburg rose comb turns slightly upward

In addition to single combs and rose combs, there are the following types of combs in other breeds pea combs in Brahmas, Cornish, and Sumatras, cushion combs in Chanteclers, strawberry combs in Malay Bantams, V-shaped or duplex combs in Houdans, Polish, and Sultans

Single Comb The results of numerous crosses, reported by Punnett (1923) and others, between birds with single combs and birds with rose combs show that the gene for single comb is recessive to the gene for rose comb Also, it has been shown that the gene for single comb is recessive to the gene for pea comb In connection with the latter cross, Punnett pointed out that, although some of the heterozygous pea combs appeared to be single combs, the fact that they were pea combs was demonstrated when these heterozygous birds were mated to birds having rose combs

Modifying Genes A side sprig is a well-defined pointed growth on the side of a single comb The presence of a side sprig on a single comb disqualifies a bird from winning a prize at poultry shows that are judged according to the provisions of the Standard of Perfection published by the American Poultry Association

Asmundson (1926) secured results with White Leghorns which indicated that side sprigs are due to the interaction of two autosomal dominant genes which are complementary in their action Taylor (1946) concluded that multiple genes, some with complementary action, were not only responsible for the production of side sprigs but were also involved in the production of multiplex combs for which he selected (see Fig 51) Alder (1946) showed that, by selective breeding of rose comb birds × rose-comb birds for six generations, some birds were secured whose combs resembled single combs to a marked degree Alder's results also indicated that the number of points on single combs is due to modifying genes Since side sprigs are caused by autosomal

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one of the parents must have been heterozygous for rose comb, or Rr In order to eliminate the gene for single comb from the flock, all suspected parents should be tested by mating them to single-comb or rr birds Should such matings produce any single-comb progeny, the suspected parent was, of course, Rr and should be discarded from the breeding pen

Pea Comb A pea comb has the appearance of three small single combs parallel with one another and joined at the base, each having

F₁ gametes of male origin

		RP	Rp	rP	rp
F₁ gametes of female origin	**RP**	RRPP Walnut	RRPp Walnut	RrPP Walnut	RrPp Walnut
	Rp	RRPp Walnut	RRpp Rose	RrPp Walnut	Rrpp Rose
	rP	RrPP Walnut	RrPp Walnut	rrPP Pea	rrPp Pea
	rp	RrPp Walnut	Rrpp Rose	rrPp Pea	rrpp Single

FIG 52 Showing the F_2 results secured from an original cross of rose comb X pea comb The F_1 birds have walnut combs, due to the interaction of the gene R, for rose comb, and the gene P, for pea comb When the F_1 birds are mated among themselves, an F_2 ratio of 9 walnut 3 rose 3 pea 1 single is the result

points, those of the two outer rows being smaller than the points of the middle row Pea comb, the gene for which is designated P, is less completely dominant to single comb than the gene R Modifying genes are involved in determining variations in number of points and the size of the two outside ridges

Munro and Kosin (1940) made the interesting observation that a peculiar ridgelike formation on the breast was characteristic of Brahmas, Cornish, Cornish Bantams, and Black Sumatras, all of which have pea combs Also, all crossbred birds with pea combs had the same sort of "breast ridge," but it was not present in any bird with other types of combs

Walnut Comb The walnut type of comb is similar to the cushion comb of the Chantecler and the strawberry comb of the Malay Bantams Walnut combs are relatively small in size and have irregular grooves on the surface

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		RP	Rp	rP	rp
	RP	RRPP Walnut	RRPp Walnut	RrPP Walnut	RrPp Walnut
F₁ gametes of female origin	Rp	RRPp Walnut	RRpp Rose	RrPp Walnut	Rrpp Rose
	rP	RrPP Walnut	RrPp Walnut	rrPP Pea	rrPp Pea
	rp	RrPp Walnut	Rrpp Rose	rrPp Pea	rrpp Single

Fig. 52. Showing the F₂ results secured from an original cross of rose comb X pea comb. The F₁ birds have walnut combs, due to the interaction of the gene R, for rose comb, and the gene P, for pea comb. When the F₁ birds ($RrPp$) are mated among themselves, an F₂ ratio of 9 walnut : 3 rose : 3 pea : 1 single is the result

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Walnut Comb. The walnut type of comb is similar to the cushion comb of the Chantecler and the strawberry comb of the Malay Bantams. Walnut combs are relatively small in size and have irregular grooves on the surface.

ancestry. Types 3 and 4 are hereditary and are recessive to normal beaks. Crossings involving types **3** and **4** produced progeny with normal beaks.

Abnormal or Missing Maxillae. Asmundson (1936), among the progeny of White Leghorn inbred matings, observed some chicks in which the maxillae of the upper beak were either reduced in size or were missing. The upper beak was frequently bent to one side, and in some of these cases the nasal bones were reduced in size. Embryonic development apparently was not affected, but the chicks could not release themselves from their shells without assistance. All that were aided died within a few days. The condition is due to an autosomal recessive gene, *mx* (Hutt 1949), and is lethal in the homozygous state.

Short Upper Beak. Landauer (1946) recorded the appearance of short upper beaks among the progeny of Mottled Houdan matings. Not only was the upper beak shortened, the degree of shortening varying widely, but also the long bones of the body were shortened, the leg bones being affected more severely than the wing bones. Embryonic mortality prior to the eighteenth day of incubation was not affected, although some embryos showed the defect as early as the ninth day of incubation.

Crossing his Mottled Houdans with White Leghorns, in which the short upper beak condition has never been recorded, led Landauer to the discovery that White Leghorns carry modifying genes that suppress the effect of the gene responsible for the short upper beak. The gene responsible for this condition is a semilethal autosomal recessive, the symbol for which Hutt (1949) designated *su*.

Missing Mandible. Marble, Hammers, and Harper (1942) and Marble, Harper, and Hammers (1944), in inbred White Leghorn stock, described chicks exhibiting cerebral hernia, abnormal eyes, a reduction in the size of other facial parts, reduced length of the upper beak, and a mere vestige of the lower mandible. All embryos homozygous for the gene die.

Short Lower Mandible. McGibbon (1946) observed shortened lower mandibles, rarely more than one-half as long as the upper beaks, among progeny secured from certain White Leghorn matings. In many respects this condition resembles the "parrot-beak" condition discussed under the next heading, although in this case there were no gross abnormalities of the long bones of the body. The gene for short lower mandible is semilethal in its effect; approximately one-half of the embryos died before the end of the incubation period was over, and of those which hatched most died soon thereafter. A few lived up to 6 months but were unable to eat or drink, largely because the short lower mandi-

ancestry. Types 3 and 4 are hereditary and are recessive to normal beaks. Crossings involving types 3 and 4 produced progeny with normal beaks.

Abnormal or Missing Maxillae. Asmundson (1936), among the progeny of White Leghorn inbred matings, observed some chicks in which the maxillae of the upper beak were either reduced in size or were missing. The upper beak was frequently bent to one side, and in some of these cases the nasal bones were reduced in size. Embryonic development apparently was not affected, but the chicks could not release themselves from their shells without assistance. All that were aided died within a few days. The condition is due to an autosomal recessive gene, *mx* (Hutt 1949), and is lethal in the homozygous state.

Short Upper Beak. Landauer (1946) recorded the appearance of short upper beaks among the progeny of Mottled Houdan matings. Not only was the upper beak shortened, the degree of shortening varying widely, but also the long bones of the body were shortened, the leg bones being affected more severely than the wing bones. Embryonic mortality prior to the eighteenth day of incubation was not affected, although some embryos showed the defect as early as the ninth day of incubation.

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resemble the forefeet of moles hence the name "talpid embryo (from *talpa,* meaning mole) Figure 54 shows the effects of the talpid gene in an 11-day-old embryo The proximal bones of the legs and wings are extremely short and there is duplication of the distal bones Each foot may have as many as ten digits fused together, and the fused digits of each wing give it the appearance of a hand Other abnormalities include reduction in the development of feather papillae, shortened beaks and vertebral column, and eversion of the viscera

Fig 54 Left showing effects of talpid gene in an 11 day old embryo Center normal embryo of same age (Cole 1942) Right double recessive micromelia in embryo showing parrot beak and deformed lower mandible (Asmundson 1942)

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wings, kidneys, and feathers have one feature in common, an epithelial layer being involved in their formation Hutt (1949) designated the symbol *wg* for the autosomal recessive gene involved.

Split Sternum. MacLaury, Buckner, and Insko (1948) described a 10-week-old White Leghorn cockerel that had an abnormally developed caudal median projection of the sternum The central portion of the sternum was very broad but was divided to form two ends (see Fig 56) instead of being straight and swordlike in shape

Fig. 56. Left, normal keel Center, bifid keel (MacLaury, Buckner, and Insko, Jr , 1948) Right, crooked keel (Waters, 1919)

Crooked Keel. The crooked-keel condition sometimes attains serious proportions in certain flocks and is of economic importance from the standpoint of the appearance of fowl and roasters dressed for market The condition is apparently not of serious concern to broiler producers because marked crookedness of the keel usually does not develop until after the .... chick broiler and fryers are sold and, in addition, most

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breeding reared at two different places but the results secured certainly indicate that rearing methods were a factor

Progeny Testing to Eliminate the Condition Since there are so many degrees of crookedness of keel and since multiple genes obviously are involved, the only rational breeding program to follow in attempting to eliminate the condition from a flock is progeny testing Numerous matings would be necessary, and goodly numbers of progeny from each mating would be desirable

Unilateral Kidney Jeffrey, Beaudette, and Hudson (1937) described a condition of kidney abnormality in a strain of White Leghorns in which the left kidney was either atrophied or missing entirely Apparently the condition is inherited but the mode of inheritance has not been determined

Crooked Neck. Jull and Quinn (1931), in breeding Brown Leghorns, observed that the progeny of three dams in one breeding pen had twisted necks, a condition which first became apparent when the birds were about half grown and gradually became more severe (see Fig 58) Some of the pullets laid a few eggs but since mating was impossible a backcross and an F_2 generation could not be secured Apparently an autosomal recessive gene was responsible for the condition

Crooked-Neck Dwarf From matings of New Hampshires Asmundson (1945) obtained some embryos about one half normal size and with

Fig 57 Left a crooked neck dwarf embryo Right normal embryo (Asmundson 1945)

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smaller than normal females   This type of dwarfism is caused by a sex-linked recessive gene, *dw*

Autosomal Dwarfism. One of the earliest reports of dwarfism in the larger breeds of chickens was that of Landauer (1929)   Among those who have studied dwarfism and reported on its inheritance most extensively are Mayhew and Upp (1932) and Upp (1934)   In a flock of Rhode Island Reds, there appeared several birds with shortened legs, especially the tarsometatarsus, outer toes turned outwards and backwards, and bodies carried in a nearly horizontal position   In some cases the head was quite broad and the beak was bent downward   From the breeding data, it was suggested that this type of dwarfism is due to an autosomal recessive gene, the dwarfs being homozygous   Landauer's Rhode Island Red dwarf was observed to have an enlarged thyroid hence the term "thyrogenous dwarfism," suggested by Landauer   Hutt (1949) suggested the symbol *td* for the gene causing this condition

Creeper. There are different names for the Creeper fowl in various countries   In Great Britain they are known as Scotch Dumpies, in France as *Courtes Pattes,* and in Germany as *Kruperhuhn*   A Creeper fowl is shown in Fig 58   Investigational work has disclosed that these Creeper fowls are of the same genetic constitution

Creepers have two peculiar characters that distinguish them from all other breeds of chickens   The wing and leg bones are very much shortened, the development of the leg bones differing markedly from those in normal breeds   Cutler (1925) pointed out that all the leg bones, except the fibula, are correspondingly shortened, that of the tibia is usually bent considerably, and the fibula is much better developed than in normal birds   Cutler suggested that all adult Creepers are heterozygous for the gene that determines the peculiar character because homozygous individuals die early

Landauer and Dunn (1930b), who used Creepers from America, Germany, Scotland, and the Marquesas Islands, studied the genetics of the "creeper" character and found that all these birds are affected by the same gene   Landauer (1942) showed that the Japanese Bantam breed carries the same gene or an allele of it   It was found, however, that relatively more homozygous embryos generally survive to late stages of embryonic development than in the case of homozygous Creeper embryos   Landauer suggested, therefore, "that the modified effect of the Creeper mutation in Japanese Bantams is caused by an incompletely dominant modifier linked with the Creeper character '

Landauer (1932) concluded that the autosomal dominant gene responsible for the Creeper character brought about a general retardation of body growth at a definite stage of embryonic development

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Fig 58 A, a rumpless bird (Ogiwara, 1928) B, hereditary crooked toes (Hicks, Jr, and Lerner, 1949). C, a German Creeper (Landauer and Dunn, 1930 *b*) D a crooked-neck bird (U. S Dept Agr)

Four Types of Rumplessness. According to the work of Landauer and Dunn (1925), Landauer (1928), Dunn and Landauer (1931, 1936), and Landauer (1945a), the four types of rumplessness include (1) accidental or sporadic rumplessness; (2) hereditary complete rumplessness due to an autosomal dominant gene Rp, (3) hereditary intermediate rumplessness due to modifying genes; (4) hereditary recessive rumplessness due to autosomal $rp 2$, the degree of recessive rumplessness being determined by modifying genes.

It is practically impossible to distinguish accidentally rumpless birds from hereditarily completely rumpless birds, and it is also practically

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may be absent but are usually fused together and the uropygial gland is either absent or rudimentary The important difference, however, is that the fused caudal vertebrae usually curve downward, and this condition is often associated with curvature of the spine

The gene *rp 2* is not completely recessive and is affected by modifying genes

Crooked Toes. Hicks and Lerner (1949) selected for a crooked-toe condition, shown in Fig 58, that proved to be hereditary Over a period of 6 years they succeeded in increasing the incidence of the condition in the selected line from about 15 per cent to over 97 per cent The elimination of birds with this condition from the regular breeding flock each year should maintain the defect at a relatively low level in the progeny

Polydactyly. By polydactyly is meant the presence of one or more extra digits (see Fig 59) Certain breeds of chickens have five toes on

Fig 59 Three forms of polydactyly Left the type of foot usually found in polydactylous breeds Center, a type often found in homozygous duplicates Right an extreme duplicate that deforms the chick to a lethal degree (Warren 1941b)

each foot instead of four, which is the number common to most breeds Five-toed breeds include Houdans, Dorkings, and Silkies

The fifth toe is a duplication of the hallux or first toe There are numerous types of polydactylism but, since the condition is of slight interest to poultry breeders in most countries except when hatchability is lowered, a brief discussion should suffice Students interested in the numerous and complex details involved should consult the literature references cited Landauer (1948), and Warren (1941 1944)

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longer medial supernumerary toe longer than the other two, great variability in the size of the middle toe, and a shortened maxilla (see Fig. 60). In some embryos, in addition to the extra toes, supernumerary metatarsal bones are present, the number of these being very variable. In addition to these common abnormalities, numerous other variations occur, such as shortened femur, tibia, and tarsometatarsus, and supernumerary structures in the wing.

Fig 60 Left, normal embryo Center, diplopod embryo. Right, diplopod embryo showing unusually complex structure of the extra wing complements (Taylor and Gunns, 1947)

The shortening and curvature of the leg bones and the upper-beak defect are probably largely responsible for the very high in-shell embryo mortality.

Diplopodia is inherited as a simple autosomal recessive gene, designated *dp* by Hutt (1949) It was suggested by Taylor and Gunns that modifying genes or environmental factors tend to suppress the action of *dp*.

Brachydactyly. By brachydactyly is meant a shortening of the fourth toe so that it is as short as or shorter than the second toe, whereas in normal birds the fourth toe is about 10 to 12 per cent longer than the second toe (see Fig. 61) Warren (1940) studied the inheritance of brachydactyly in crossbred stock descended from Light Brahmas and Silkies, both of which have feathered shanks Jaap (1939) and Warren (1940) observed that brachydactylism and shank feathering are associated. Warren found that the extent of shank feathering bore a direct relation to the degree of shortening of the fourth toe Considerable variation was observed in the degree of the expression of brachy-

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Matings of defective × normal birds gave a preponderance of normal birds in the progeny. Matings of defective × defective birds gave approximately equal numbers of defective and normal birds in the progeny. The results secured from these and other matings led to the conclusion that several genes are necessary for the expression of ungual osteodystrophy and that some of these genes act as modifiers.

Syndactyly. In swimming birds a web of skin unites the toes, hence the term "syndactyly." Webbing of the feet to the same extent found

Fig 62   Syndactylism   (Warren 1950)

in swimming birds is not a normal characteristic of chickens. Warren (1950), however, observed a few White Plymouth Rocks showing pronounced syndactylism (see Fig 62). In most of what few cases appeared, both feet were webbed. Also, the extent of webbing varied considerably.

Danforth (1919a) and Jaap (1939) expressed the view that syndactylism and brachydactylism are caused by the same genes. Danforth believed that syndactylism and leg feathering were caused by the same genes in Light Brahmas, but it is of interest to note that White Plymouth Rocks do not have feathered legs.

Warren's F_1 generation matings produced progenies varying from none with syndactylism to 50 per cent syndactyls. No matings of syndactyls × syndactyls and of syndactyls × heterozygotes produced only syndactylous progeny. Syndactylism is not sex-linked and its mode of inheritance is very complicated.

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so that they curved downward with their tips pointing toward the shank bone. Decalcification took place relatively sooner in young cockerels than in older birds.

Goodale (1925) developed a strain of birds by selection in which about half of the females had spurs, indicating that sexual dimorphism in spur development is genetic.

FIG. 63. Left, double spur development in early adulthood. Right, double spurs in adult male. (Warren, 1946.)

Double Spurs. Warren (1946) described a double-spurred condition, shown in Fig 63, which could be identified in males and females at hatching time, the incidence among females being higher than among males. The results of different kinds of matings indicated that the gene responsible for this character behaves like a recessive

Multiple Spurs. Hutt (1941) made an original mating of a multi-spurred Black Sumatra male × White Leghorn females, all of the F_1

FIG. 64. Left, multiple spurs in Black Sumatra, showing three spurs of equal length Right, the feet of a Black Sumatra, showing four spurs on the left leg (Hutt, 1941)

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TABLE 5—*Continued*

DOMINANT AND RECESSIVE MORPHOLOGICAL CHARACTERS

Character	Dominant or Recessive	Autosomal or Sex-Linked
Ragged wing	Recessive to normal wing	Autosomal
Hen feathering in males	Dominant to normal feathering	Autosomal
Rose comb	Dominant to single comb	Autosomal
Pea comb	Dominant to single comb	Autosomal
Walnut comb	Dominant to rose, pea, and single comb	Autosomal
Blindness	Recessive to normal eye	Autosomal
Bilateral microphthalmia	Recessive to normal condition	Autosomal
Abnormal or missing maxillae	Recessive to normal condition	Autosomal
Short upper beak	Recessive to normal beak	Autosomal
Missing mandible	Recessive to normal condition	Autosomal
Short mandible	Recessive to normal condition	Autosomal
Hereditary chondro-dystrophy	Recessive to normal condition	Autosomal
Micromelia	Two pairs complementary recessives	Autosomal
Winglessness	Recessive to normal wings	Autosomal
Crooked neck dwarf	Recessive to normal condition	Autosomal
Dark Cornish short leg	Dominant to normal condition	Autosomal
Sex-linked dwarfism	Recessive to normal condition	Sex-linked
Autosomal dwarfism	Recessive to normal condition	Autosomal
Creeper	Dominant to normal condition	Autosomal
Hereditary complete rumplessness	Dominant to normal condition	Autosomal
Hereditary recessive rumplessness	Recessive to normal condition	Autosomal
Talpid embryos	Recessive to normal condition	Autosomal
Polydactyly	Dominant to four toed condition	Autosomal
Diplopodia	Recessive to four toed condition	Autosomal
Brachydactyly	Dominant to normal condition	Autosomal
Multiple spurs	Dominant to single spurs	Autosomal
Divided uropygial gland papilla	Dominant to normal condition	Autosomal

PROBLEMS

1 What is the difference between silky and frizzled plumage and what respective genes involved are responsible for these types of plumage?

2 Tell what genes are responsible for frayed feathering, flightlessness, ragged wing, stringy feathers, and ropy feathers and describe each condition

3 What is the difference between nakedness and apterylosis?

4 Discuss the inheritance of congenital baldness and crest

5 Discuss the relationship among the following three traits, early, late, and slow feathering

6 What type of comb will the offspring of each of the following matings possess?

$Rr\ pp \times rr\ Pp$	$Rr\ pp \times rr\ Pp$
$RR\ Pp \times rr\ Pp$	$rr\ PP \times Rr\ Pp$
$Rr\ Pp \times Rr\ pp$	$Rr\ Pp \times Rr\ Pp$
$rr\ PP \times Rr\ pp$	$rr\ Pp \times Rr\ PP$

TABLE 5—*Continued*

DOMINANT AND RECESSIVE MORPHOLOGICAL CHARACTERS

Character	Dominant or Recessive	Autosomal or Sex-Linked
Ragged wing	Recessive to normal wing	Autosomal
Hen feathering in males	Dominant to normal feathering	Autosomal
Rose comb	Dominant to single comb	Autosomal
Pea comb	Dominant to single comb	Autosomal
Walnut comb	Dominant to rose, pea, and single comb	Autosomal
Blindness	Recessive to normal eye	Autosomal
Bilateral microphthalmia	Recessive to normal condition	Autosomal
Abnormal or missing maxillae	Recessive to normal condition	Autosomal
Short upper beak	Recessive to normal beak	Autosomal
Missing mandible	Recessive to normal condition	Autosomal
Short mandible	Recessive to normal condition	Autosomal
Hereditary chondro-dystrophy	Recessive to normal condition	Autosomal
Micromelia	Two pairs complementary recessives	Autosomal
Winglessness	Recessive to normal wings	Autosomal
Crooked neck dwarf	Recessive to normal condition	Autosomal
Dark Cornish short leg	Dominant to normal condition	Autosomal
Sex-linked dwarfism	Recessive to normal condition	Sex-linked
Autosomal dwarfism	Recessive to normal condition	Autosomal
Creeper	Dominant to normal condition	Autosomal
Hereditary complete rumplessness	Dominant to normal condition	Autosomal
Hereditary recessive rumplessness	Recessive to normal condition	Autosomal
Talpid embryos	Recessive to normal condition	Autosomal
Polydactyly	Dominant to four toed condition	Autosomal
Diplopodia	Recessive to four toed condition	Autosomal
Brachydactyly	Dominant to normal condition	Autosomal
Multiple spurs	Dominant to single spurs	Autosomal
Divided uropygial gland papilla	Dominant to normal condition	Autosomal

PROBLEMS

1 What is the difference between silky and frizzled plumage and what respective genes involved are responsible for these types of plumage?

2 Tell what genes are responsible for frayed feathering, flightlessness, ragged wing, stringy feathers, and ropy feathers and describe each condition

3 What is the difference between nakedness and apterylosis?

4 Discuss the inheritance of congenital baldness and crest

5 Discuss the relationship among the following three traits: early, late, and slow feathering

6 What type of comb will the offspring of each of the following matings possess?

$$Rr\ pp\ \times rr\ Pp \qquad\qquad Rr\ pp\ \times rr\ Pp$$
$$RR\ Pp\ \times rr\ Pp \qquad\qquad rr\ PP\ \times Rr\ Pp$$
$$Rr\ Pp\ \times Rr\ pp \qquad\qquad Rr\ Pp\ \times Rr\ Pp$$
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6 · Gene Linkage and
Blood Group Antigens

In this chapter is presented a brief discussion of two rather specialized fields of work of somewhat limited interest to most readers of this book. Determining linkages is of fundamental importance to geneticists, and, although up to the present most of the linkages that have been determined pertain to genes of relatively little significance to the great majority of poultry breeders, the day may come when some of these genes are shown to be linked with genes affecting quantitative characters. The problem of blood group antigens opens up a new field of investigation, the results of which some day may have considerable significance in certain aspects of poultry breeding.

LINKAGE

One of the fundamental principles of Mendelian inheritance—the independent assortment of the genes—has been fully discussed in Chapter 3. Dominance and recessiveness have been shown to be clear-cut in many characters. The independent assortment of the genes has also been found to hold good in respect to many pairs of genes, giving the 3 : 1, the 9 : 3 : 3 : 1, and other ratios in the F_2 generations.

On the other hand, many cases have been established in which independent assortment of the genes does not take place, so that in the F_2 generation a normal Mendelian ratio is not obtained. In several instances in the domestic fowl when parents differing in two pairs of characters have been crossed, the F_2 generation, instead of consisting of a 9 : 3 : 3 : 1 ratio, contains an excess of birds having the same combination of characters as the original parents and a relatively small number of birds showing the new combination of characters.

The Principle of Linkage. These apparently abnormal F_2 ratios are due to the phenomenon known as linkage, which means simply that genes giving rise to certain characters tend to remain together instead of assorting themselves independently of each other when the gametes

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The Principle of Linkage. These apparently abnormal F_2 ratios are due to the phenomenon known as linkage, which means simply that genes giving rise to certain characters tend to remain together instead of assorting themselves independently of each other when the gametes

Owing to the fact that some characters are dominant over others, the F_2 ratio does not give a direct index of the kinds of gametes produced by the birds of the F_1 generation in cases of linkage. But a backcross of an F_1 bird heterozygous for each of two pairs of genes to the parent with both pairs of genes in a homozygous recessive condition provides an accurate index of the constitution of the gametes of the heterozygous F_1 bird

The Principle of Crossing Over. Genes that are located in the same chromosome, whether it be autosome or sex chromosome, should always be inherited together as linked genes if the chromosome remains intact in inheritance. But it has been observed previously that linkage is rarely complete, thus indicating that frequently the chromosome is not inherited intact. Investigational work has established the fact that the gametes go through various stages of development and division in order that a gamete from the male may unite with a gamete from the female. During one of these stages of development, each chromosome of a pair lies side by side and, occasionally, instead of separating intact, there may be an interchange of parts of the same pair of chromosomes, hence the suggestion that crossing over takes place. The genes of one chromosome are said to cross over to the other chromosome of the pair

Determining Linkage Value The amount of crossing over that takes place is determined by the degree of linkage, or the degree of linkage is determined by the extent to which crossing over takes place. Regardless of which is cause and which is effect, crossing over is the corollary of linkage

Each pair of linked genes exhibits a characteristic proportion of noncrossovers and crossovers, the degree of linkage being determined in terms of the percentage of crossovers in the gametic series. This is called the linkage value

Under independent assortment the genes are transmitted independently of each other and the various combinations are approximately in equal numbers whereas under linkage the noncrossovers are always more numerous than the crossovers. Linkage may vary from slightly over 50 per cent to nearly 100 per cent noncrossovers of the total number of progeny. This is another way of saying that crossing over may vary from about 50 per cent to less than 1 per cent. In other words, linkage strength varies inversely as the crossover value increases

The results in the F_2 generation can be predicted for any cross involving linkage, provided that the linkage value is known, the linkage value being most readily determined by backcrossing

Owing to the fact that some characters are dominant over others, the F_2 ratio does not give a direct index of the kinds of gametes produced by the birds of the F_1 generation in cases of linkage But a backcross of an F_1 bird heterozygous for each of two pairs of genes to the parent with both pairs of genes in a homozygous recessive condition provides an accurate index of the constitution of the gametes of the heterozygous F_1 bird

The Principle of Crossing Over. Genes that are located in the same chromosome, whether it be autosome or sex chromosome, should always be inherited together as linked genes if the chromosome remains intact in inheritance But as has been observed previously that linkage is rarely complete, tbus indicating that frequently the chromosome is not inherited intact Investigational work has established the fact that the gametes go through various stages of development and division in order that a gamete from the male may unite with a gamete from the female During one of these stages of development, each chromosome of a pair lies side by side and, occasionally, instead of separating intact, there may be an interchange of parts of the same pair of chromosomes, hence the suggestion that crossing over takes place The genes of one chromosome are said to cross over to the other chromosome of the pair

Determining Linkage Value The amount of crossing over that takes place is determined by the degree of linkage, or the degree of linkage is determined by the extent to which crossing over takes place Regardless of which is cause and which is effect, crossing over is the corollary of linkage

Each pair of linked genes exhibits a characteristic proportion of noncrossovers and crossovers, the degree of linkage being determined in terms of the percentage of crossovers in the gametic series This is called the linkage value

Under independent assortment the genes are transmitted independently of each other and the various combinations are approximately in equal numbers whereas under linkage the noncrossovers are always more numerous than the crossovers Linkage may vary from slightly over 50 per cent to nearly 100 per cent noncrossovers of the total number of progeny This is another way of saying that crossing over may vary from about 50 per cent to less than 1 per cent In other words, linkage strength varies inversely as the crossover value increases

The results in the F_2 generation can be predicted for any cross involving linkage, provided that the linkage value is known, the linkage value being most readily determined by backcrossing

FIG 65   The arrangement of some genes on five autosomes, A to E, and on the sex chromosome, F

Fig 65 The arrangement of some genes on five autosomes, A to L, and on the sex chromosome, Γ

comb, the crossing-over percentage being as low as 0 38 per cent   The genes involved are, therefore, close together on the chromosome

The results of studies conducted by Taylor (1934) on linkage between the genes for Creeper and single comb are in close agreement with those of Landauer   Taylor observed 0 59 per cent crossing over in Creeper females and 0 40 per cent crossing over in Creeper males   The results secured by Landauer and Taylor confirm the observation on linkage between these genes originally made by Serebrovsky and Petrov (1928), although their results indicated approximately 8 per cent crossing over Of the total number of 9494 gametes tested by Landauer and Taylor there were 38 crossovers, giving a crossing-over percentage of 0 4

Hutt (1932) described a mutation of the uropygial gland, the dominant gene *U* causing a division of the papillae of the gland   Hutt (1936) observed a crossing-over percentage of 29 6 between the *U* and *R*, the gene for rose comb (see Fig 65B)   The genes for Creeper, rose comb, and the uropygial mutation are linked together, the Creeper and comb genes being very close together, but which is nearest the uropygial mutant gene has not been determined

In Fig 65 are shown the proposed arrangements of groups of genes on each of six different chromosomes, including groups A and B, which have already been mentioned   Groups A to E, inclusive, represent linkage groups in five autosomes   Group F represents a linkage group in the sex chromosome

In autosome A, the linkage group includes *Cr*, crest, *I*, dominant white as in White Leghorns, *F*, frizzled plumage

In autosome B, the linkage group is *Cp*, Creeper, *R*, rose comb, *U*, divided uropygial papillae

In autosome C, the linkage group includes *D*, duplex comb, *M*, multiple spurs, *Po*, polydactyly, *Po^d*, duplicate polydactyly

In autosome D, the linkage group includes *h*, silky, and *Fl*, flightless

In autosome E, the linkage group includes *O*, blue egg, *P*, pea comb, *ma*, marbling, *Na*, naked-neck, although Warren (1938) stated that *Na* is in the D group with *h* and *Fl*

In sex chromosome F, the linkage group includes *Ko*, no head streak, *sd*, diluted color, *B*, barring as in Barred Plymouth Rocks, *Id*, inhibitor of dermal melanin, *Br*, brown eye, *La*, light down, *S*, silver, *K*, late feathering

Those interested in this specialized subject of linkage should consult the literature references cited at the end of this chapter, especially Hutt (1949) and Warren (1949)

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In autosome C, the linkage group includes D, duplex comb, M, multiple spurs, Po, polydactyly, Po^d, duplicate polydactyly

In autosome D, the linkage group includes h, silky, and Fl, flightless

In autosome E, the linkage group includes O, blue egg, P, pea comb, ma, marbling, Na, naked-neck, although Warren (1938) stated that Na is in the D group with h and Fl

In sex chromosome F, the linkage group includes Ko, no head streak, sd, diluted color, B, barring as in Barred Plymouth Rocks, Id, inhibitor of dermal melanin, Br, brown eye, Lt, light down, S, silver, K, late feathering

Those interested in this specialized subject of linkage should consult the literature references cited at the end of this chapter, especially Hutt (1949) and Warren (1949)

PROBLEMS

1 What is the relationship between linkage and crossing over?

2 Outline a breeding project with a view to determining the linkage strength between two genes whose linkage strength has not yet been determined

3 What is the relationship between two genes when (1) there is no crossing over and when (2) there is 50 per cent crossing over?

4 From the information given concerning the numbers of chromosomes in the domestic fowl, how many linkage groups should it be possible to establish in the male and in the female?

5 What are some of the practical aspects involved in linkage?

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7 · Fertility
and Hatchability

The economic loss resulting from poor fertility and low hatchability in breeding flocks in the United States amounts to several million dollars every year. Except for their use as fertilizer or for certain other purposes, infertile eggs and dead embryos have practically no salvage value. Whatever can be done, therefore, to secure a higher percentage of fertility in hatching eggs and a higher percentage of hatchability of the fertile eggs should be of direct benefit to poultry breeders and hatchery operators.

FERTILITY

Many factors affect fertility, several of them under the control of the poultry breeder whether he be a pedigree breeder or a hatchery flock owner. Factors affecting semen production and its quality and the site of fertilization have been discussed in Chapter 3. The discussion in this chapter pertains largely to factors affecting the percentage of fertile eggs produced under different conditions.

Detecting Fertility. Olsen and Knox (1938) demonstrated that the fertility of incubated eggs could be detected after 3 hours of incubation. Kosin (1944, 1945a) developed techniques for detecting fertility in broken-out unincubated eggs by examining the "germ spot" with the naked eye or under the microscope, after fixation and staining with alum cochineal. In infertile eggs the blastodiscs show signs of disintegration, whereas in fertile eggs the blastoderm is in a relatively rapid state of development. Kosin (1945b) showed that in infertile eggs parthenogenic cleavage occurs quite frequently.

Gowe (1950), using Kosin's technique slightly modified, was able to distinguish fertile from infertile eggs with a high degree of accuracy. He showed that blastoderms which had degenerated and died before oviposition occurred appeared as blastodiscs characteristic of infertile eggs, thus confirming the original observation of Munro and Kosin (1945) and Blyth (1945). The Kosin and Gowe techniques should be

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males exposed to 12 or more hours of light daily made significantly greater gains in semen production than males exposed to less than 1 hour of light daily

Nutrition. Under normal conditions with properly balanced diets, fertility is not liable to be adversely affected   However, greatly reduced feed consumption for a considerable period will reduce fertility to a marked extent, as Parker and McSpadden (1943b) have shown

Hormones. According to the results secured by Shoffner and Smyth (1944) and Hays (1945), sexually inactive males may be stimulated by the gonad-stimulating hormone in pregnant mare's serum   Andrews and Schnetzler (1945) and McCartney and Shaffner (1950) observed that feeding hens a ration containing 0 2 per cent thiouracil had no adverse effect upon fertility   On the other hand, reduced fertilizing capacity of the semen of males treated with thiouracil was observed by Shaffner and Andrews (1948)   Similar results were reported by Shaffner (1948) for males fed thyroprotein, although this was not confirmed by Huston and Wheeler (1949)   The fertility of eggs produced by hens fed thyroprotein was not adversely affected, according to Wheeler and Hoffmann (1948) and McCartney and Shaffner (1950)

Males in Batteries and Coops   Parker, McKenzie, and Kempster (1940) observed that breeding males kept in batteries were less active sexually than males kept in breeding pens   Palafox (1948) obtained a fertility of 60 1 per cent of eggs laid by White Leghorn pullets that were mated to cockerels kept in wire-floored coops and 80 3 per cent fertility from the same pullets mated to males in breeding pens

Age of Breeders. That fertility tends to decline with increasing age of the breeding stock is the general experience of poultry breeders   Observations at various research centers vary somewhat, limited numbers of birds apparently being a factor in some cases   Results secured by Martin and Insko (1934), Jull (1935b), Hays and Sanborn (1939) and Insko, Steele, and Wightman (1947) indicate that fertility apparently decreases relatively more rapidly with increasing age after the first year in males than in females

Social Dominance. Every breeding flock has its own social organization   Guhl, Collias, and Allee (1945) and Guhl and Warren (1946) demonstrated that socially dominant males mated more frequently and sired more offspring than did their socially inferior brethren

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Is Fertility Inherited? The problem of determining whether fertility is inherited is complicated by the fact that fertility is affected by several environmental factors and by the individuality of the breeding males and females Also, some of the differences of opinion that have been held with respect to the inheritance of fertility may have been due to the fact that in some cases eggs containing dead blastoderms were classified as infertile eggs

The data of Jull (1935a) and Blyth (1945) indicated that fertility is inherited On the other hand, the results secured by Hays (1950) and several earlier investigators indicated that fertility is not inherited According to Bernier, Taylor, and Gunns (1951), "The fertility of matings appears to be a property of the parents and not of the prospective zygotes resulting from the mating" At any rate, except for eliminating certain low-fertility individual males and females from breeding pens, it is doubtful whether the fertility factor should be included in a poultry breeder s program of family selection and progeny testing

White Wyandottes. Hutt (1940) suggested that the relatively low fertility often encountered in White Wyandottes is probably due to the fact that a relatively higher number of individuals give very low fertility as compared with other breeds Munro (1946), while agreeing that White Wyandottes on the average are relatively poorer in fertility than some other breeds was of the opinion that, among the strains of White Wyandottes he studied, environmental factors were more important than inheritance with respect to differences in fertility It seems possible that the relatively short back characteristic of exhibition-type White Wyandottes, may have been a factor involved in low fertility in certain strains studied Both Hutt and Munro showed that some strains of White Wyandottes were quite high in fertility Many White Wyandotte flocks in Arkansas kept for the production of hatching eggs for broiler chicks give good fertility

Selective Fertilization Observations of various workers (Bonnier and Trulsson 1939a, Pyenson 1939, and Parker, McKenzie, and Kempster 1942) indicate quite clearly that in certain cases the eggs of a female may be fertilized readily by the sperm of one male but not by the sperm of another male

Artificial Insemination The procedures involved in securing semen from males and inseminating females have been described by Quinn and Burrows (1936) and Burrows and Quinn (1937 1938 1939) Parker (1939) described an avian semen collector Wheeler (1948) described a one-man technique for collecting chicken semen thus saving one man s time as compared with the Burrows and Quinn technique which requires the services of two men

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son and Warren (1936), Hays and Sanborn (1939), and Lamoreux (1940) are sufficient to show that the pedigree breeder should consider the possibility that relatively low fertility in a single-male breeding flock may be due to excessive infertility on the part of certain females.

Stud mating, which consists in mating females to a male kept in a coop, would be one means of overcoming the problem of low fertility due to preferential matings. Nicolaides (1934) reported as good fertility from stud matings as from pen matings, but Bird (1937), Jeffrey (1944), and others have reported relatively unsatisfactory results from stud matings.

Multiple-male breeding flocks consist of several males mated to varying numbers of females. Too many males in the flock may actually result in decreased fertility because of excessive fighting. Byerly and A. B. Godfrey (1937) reported that, beyond a minimum of about fifteen, as number of females per male increased, fertility tended to decrease in a linear fashion. Parker and Bernier (1950), reported two cases in which a single New Hampshire cockerel gave 73 and 83 per cent fertility, respectively, when mated to approximately 100 females; these were exceptional cases. In several instances, as few as three to five cockerels gave over 90 per cent fertility, but it was observed that in order to maintain a satisfactory level of fertility it was necessary to use six to seven cockerels per 100 females.

Onset and Duration of Fertility in Natural Matings. That a fertile egg may be produced shortly after copulation takes place has been demonstrated by the following investigators, the number of hours

Fig. 66 The period of time required to secure maximum fertility, from the time the males were placed in the breeding pens, in relation to the number of males per 100 females, New Hampshires. (Parker and Bernier, 1950.)

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uate more precisely than previous investigations the precise relationship between fertility and hatchability, indicate that hatchability and fertility are biologically independent.

Egg Size. The fact that the largest eggs produced by a flock usually give a lower percentage of hatchability than the average size of egg for the flock was demonstrated by Warren (1934) and A. B. Godfrey (1936). Other investigators have shown that very small eggs hatch poorly but that eggs somewhat smaller than the mean egg size of the flock hatched better than excessively large eggs. Skoglund, Tomhave, and Mumford (1948), in a study involving over 25,000 New Hampshire fertile eggs, secured the following results:

Egg size, ounces per dozen	18	20	22	24	26	28	30
Percentage of fertile eggs hatched	69	88	90	92	89	86	78

Olsen and Haynes (1949), in a study of White Leghorn eggs, obtained a hatchability of approximately 71 per cent from eggs weighing 65 grams or more, 80 per cent from eggs weighing 45 grams or less, as compared with approximately 87 per cent from eggs weighing from 46 to 64 grams. It need only be mentioned here that a 2-ounce egg (24 ounces per dozen) is equivalent to 56.7 grams.

Egg Shape. Marble (1943) pointed out that egg shape is quite uniform for eggs laid by an individual bird. Variations in shape that normally occur among the eggs of a hen do not affect hatchability, as shown by Jull and Haynes (1925), Hays and Sumbardo (1927), and Skoglund (1951). Olsen and Haynes (1949), however, secured a hatchability of only 49 per cent from misshapen eggs, as compared with a hatchability of 87 per cent from normally shaped eggs laid by the same flock.

Proportion of Albumen to Yolk. Scott and Warren (1941) observed that eggs in which the proportion of albumen to yolk was 2 to 1 gave a better hatchability than eggs which had a higher or lower proportion of these two parts of the egg.

Egg Faults. Halnan (1935) stated that the tendency to lay eggs with faults, such as large air cells and weak shells, appeared to be characteristic of certain birds and strains. Olsen and Haynes (1949) determined the hatchability of each of the five following classes of eggs laid by a White Leghorn flock: (1) eggs with poor shells, including roughness, and rough or thin areas at either end of the egg, 17 per cent; (2) eggs with large blood clots and eggs in which blood had diffused throughout the contents of the egg, 71 per cent; (3) eggs with misplaced air cells, 68 per cent; (4) eggs with loose, movable air cells, 32 per cent.

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Egg Shape. Marble (1943) pointed out that egg shape is quite uniform for eggs laid by an individual bird. Variations in shape that normally occur among the eggs of a hen do not affect hatchability, as shown by Jull and Haynes (1925), Hays and Sumbardo (1927), and Skoglund (1951). Olsen and Haynes (1949), however, secured a hatchability of only 49 per cent from misshapen eggs, as compared with a hatchability of 87 per cent from normally shaped eggs laid by the same flock.

Proportion of Albumen to Yolk. Scott and Warren (1911) observed that eggs in which the proportion of albumen to yolk was 2 to 1 gave a better hatchability than eggs which had a higher or lower proportion of these two parts of the egg.

Egg Faults. Halnan (1935) stated that the tendency to lay eggs with faults, such as large air cells and weak shells, appeared to be characteristic of certain birds and strains. Olsen and Haynes (1949) determined the hatchability of each of the five following classes of eggs laid by a White Leghorn flock: (1) eggs with poor shells, including roughness, and rough or thin areas at either end of the egg, 47 per cent; (2) eggs with large blood clots and eggs in which blood had diffused throughout the contents of the egg, 71 per cent; (3) eggs with misplaced air cells, 68 per cent; (4) eggs with loose, movable air cells, 32 per cent,

found, in general, that the darker the shade of pigment, the better the hatchability On the other hand, Brooks and Ellis (1948), quoted by Godfrey and Jaap, and Skoglund (1950) were unable to find any relationship between shell color and hatchability in high-hatching strains Funk and Forward (1949) reported the following hatchability percentages in their strain of New Hampshires Hens laying light brown-shelled eggs, 57, hens laying medium brown-shelled eggs, 68, and hens laying dark brown-shelled eggs, 77 These data indicate that the differences in hatchability were due to the genetic differences among the three groups of hens rather than to shell color

Rate of Laying. Several investigators, including Jull (1931b), Byerly, Titus, and Ellis (1933), Funk (1934), and Bernier, Taylor, and Gunns (1951) have shown that the eggs of birds that lay at a high rate just before and during the period that eggs are being incubated tend to hatch better than the eggs of birds that lay at a low rate Funk (1939) found that the eggs of hens laying from two to six eggs per clutch hatched better than the eggs of hens laying one egg per clutch Also, the eggs of hens laying four to six eggs per clutch hatched better than eggs of hens laying two eggs per clutch Hays (1938) showed that the longer the interval between clutches, usually the lower the hatchability, from which it was suggested that "birds producing clutches at frequent intervals are likely to produce eggs of high hatchability"

Position of Egg in Clutch. It was found by Bernier, Taylor, and Gunns (1951) that the hatchability of the eggs of intermediate clutch positions between the first and last eggs of clutches was significantly higher than the hatchability of the first and last eggs of clutches

Hour of Laying. The hatchability of eggs laid before 8 o'clock in the morning and after 2 o'clock in the afternoon was lower than the hatchability of eggs laid between 8 A M and 2 P M in studies made by Bernier, Taylor, and Gunns (1951)

Age of Breeders. Results secured by Hays and Sanborn (1924), Axelsson (1932), Warren (1934), Funk (1934), and Jull (1935b) are in agreement in showing that the hatchability of eggs laid by pullets is usually slightly in excess of the hatchability of yearling females Hyre and Hall (1932) compared the hatchability of the eggs of the same group of yearling females used again as 3-year-olds, 4-year-olds, 5-year-olds, respectively, and observed a slightly lower hatchability each succeeding year Similar results were secured by Hays and Talmadge (1949)

Relative Influence of Sire and Dam. Hatchability genes are transmitted by the sire and dam to their offspring, but the hatchability of eggs laid by a dam is influenced by the diets she is fed and by physiological disturbances of her own organism which affect the composition

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Relative Influence of Sire and Dam. Hatchability genes are transmitted by the sire and dam to their offspring, but the hatchability of eggs laid by a dam is influenced by the diets she is fed and by physiological disturbances of her own organism which affect the composition

The coefficient of inbreeding is a measure of the degree of relationship between sire and dam and is expressed in terms of a percentage Knox (1946) pointed out that coefficients of inbreeding serve a useful purpose as a statistical measure of the homozygosity of a large gene complex How to determine the coefficient of inbreeding is discussed in Chapter 12, together with the formula for determining the amount of inbreeding

A decline in hatchability following close inbreeding has been reported by Cole and Halpin (1916, 1922), Dunn (1923a, 1928), Goodale (1927), Warren (1927-28, 1934), Jull (1929a, 1929b), Dumon (1931), Dunkerly

Fig 67 Showing the trend in the average percentage of fertile eggs hatched for all inbreds and for those inbreds chosen to be parents, together with the number of birds in each group (Waters and Lambert 1936a)

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The deleterious effects of inbreeding on hatchability that usually result, when selective breeding for high hatchability is not practiced, have been shown to be due largely to increased embryonic mortality during the first 4 and especially the last 3 days of incubation This is borne out by the observations of Bronkhorst (1933), Byerly, Knox, and Jull (1934), and others

Shoffner (1948b) studied the effects of the intensity of inbreeding on hatchability in nine inbred lines, including White Leghorns, White Plymouth Rocks, and New Hampshires Some lines were inbred as much as 60 per cent whereas other lines approached zero inbreeding The results secured led Shoffner to conclude that for each 10 per cent increase in the coefficient of inbreeding, hatchability decreased 4.4 per cent, on the average Wilson (1948b) observed that the inbreeding of the dam seemed to have greater effect on hatchability than the inbreeding of the offspring

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Horlacher, Smith, and Wiley (1941) and Warren (1942) showed the extent to which hatchability was improved in various crossbred matings It should be kept in mind that in each of these matings only one male was used Some of their results are given in Table 6

TABLE 6

EFFECTS OF CROSSBREEDING ON HATCHABILITY

Kind of Mating	Hatchability per cent
Horlacher, Smith, and Wiley (1941)	
Rhode Island Red purebred matings	77
White Wyandotte purebred matings	79
Rhode Island White purebred matings	93
Barred Plymouth Rock purebred matings	79
White Plymouth Rock purebred matings	73
Rhode Island Red male × White Wyandotte females	83
White Wyandotte male × Rhode Island Red females	84
White Wyandotte male × Rhode Island White females	90
White Wyandotte male × White Plymouth Rock females	63
White Plymouth Rock male × Barred Plymouth Rock females	89
Warren (1942)	
White Leghorn purebred matings (strain *W*)	61
Barred Plymouth Rock male × White Leghorn females (strain *W*)	80
White Leghorn purebred matings (strain *E*)	84
Barred Plymouth Rock male × White Leghorn females (strain *E*)	86
White Leghorn purebred matings (strain *K*)	71
Barred Plymouth Rock male × White Leghorn females (strain *K*)	80

The data in Table 6 are quite consistent in showing that in most cases crossbreeding increased hatchability The 93 per cent hatchability of the Rhode Island Whites of Horlacher, Smith, and Wiley would be difficult to improve upon by crossing them with even the best inbred line available It must be kept in mind, of course, that too much emphasis should not be attached to data involving single-male mating flocks

Knox, Quinn, and A B Godfrey (1943) over a period of 4 years made several matings of purebred Rhode Island Reds, Light Sussex, and White Wyandottes and of crosses between Rhode Island Red males and Light Sussex females and between Rhode Island Red males and White Wyandotte females The hatchability percentages were as fol-

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nizable and can readily be dispensed with (embryos homozygous for the *Cp* gene never hatch)

With respect to autosomal recessive genes, it must be remembered that their presence in poultry stocks has been discovered largely through inbreeding   Under ordinary circumstances, a poultry breeder is not liable to recognize the deleterious effects of a recessive lethal gene in a homozygous state unless the embryonic mortality from a given mating is quite high   In any given mating that produces embryos which die from the effects of recessive lethals in a homozygous state, it is obvious that both parents are heterozygous for the gene   The poultry breeder who desires to eliminate the lethal from his flock should dispense with not only the "carrier" parents but also all their progeny because two-thirds of them are also heterozygous for the gene

Recessive lethal genes, by and large, are probably rather widespread in poultry stocks, and unless inbreeding is practiced they will probably have little effect on hatchability, except in the case of a recessive lethal gene having a slight semilethal effect in a heterozygous condition

Breeding to Improve Hatchability.   The discussion in the second part of this chapter has dealt with genes determining the level of hatchability and has not considered the effect on hatching results of such factors as the conditions under which eggs are held before incubation and methods of incubation

From the evidence presented in this chapter concerning the relationship between hatchability and such characters as egg size, specific gravity, shell thickness, 14-day-egg-weight loss during incubation, and rate of laying all of which are hereditary, it is apparent that many genes determine the percentage of fertile eggs that hatch   In addition lethal genes, when present in a homozygous condition, reduce hatchability   Any poultry breeder who desires to eliminate lethal genes that may be discovered in his flock would need to practice progeny testing

The results secured from different intensities of inbreeding indicate that hatchability is inherited   The results secured from crossing inbred lines show that strains and inbred lines differ with respect to the genes they carry that determine hatchability   The improvement in hatchability that usually results from crossbreeding especially when the parental breeds are noted for low hatchability, suggests quite clearly that heterosis is genetic in nature

It has been demonstrated that males differ among themselves with respect to their ability to transmit high hatchability to their progeny   Females also have been shown to differ among themselves with respect to their ability to transmit high hatchability to their progeny

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8 · Viability

In all countries, losses from disease in poultry flocks are of paramount importance, not only with respect to the birds that die after having consumed various amounts of feed, depending upon age at death, but also with respect to the monetary loss resulting from retarded growth, lower meat value, and decreased egg production of many of the birds which survive the attacks of disease organisms

Contagious and Noncontagious Diseases. A disease may be infectious or noninfectious, the difference depending upon whether the disease is due to an infectious agent The pullorum disease is infectious, whereas a disease resulting from vitamin deficiency is noninfectious From the standpoint of their transmissibility, diseases are referred to as contagious or noncontagious, the difference depending upon whether they can be transmitted to a susceptible bird Avian leukosis is a contagious disease, whereas perosis is a noncontagious disease

Three Methods of Disease Control. Three possible methods of disease control are available to poultrymen The first is sanitation The second is through the use of therapeutic agents The third is breeding for resistance to disease Hutt (1938a) observed that the major portion of the laying-pullet mortality that normally occurs is due to diseases that are not amenable to sanitation, immunization, and the elimination of carriers and exposed birds Brandly and Waters (1942) pointed out that the modern concept of disease recognizes the interdependence of the three following variables (1) the inherited capacity of the host to resist disease, (2) the relative virulence of the disease-producing organism, and (3) the environment, which may materially influence the reaction of the host and the pathogen

Breed Differences in Viability. It has been established that certain breeds differ from others with respect to their ability to withstand unfavorable environmental conditions Benedict, Landauer, and Fox (1932) showed that the homozygous Frizzle fowls lose much more body heat than normal fowls and suffer much greater mortality at very low temperatures Hutt (1938b) showed that Leghorns suffer much less mortality than general-purpose breeds when the temperature is exces-

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supplied evidence indicating that females are more viable than males Insko, Steele, and Wightman (1947) carried on a breeding program with White Leghorns and Rhode Island Reds involving females of various ages up to 7 years and males consisting mostly of cockerels Productive longevity was the primary factor studied, certain egg production, egg shape and weight, hatchability, and other qualifications serving as the bases upon which breeding stock was selected each year Egg production, fertility, and hatchability declined progressively after the first year, but those hens which qualified for several years declined less rapidly than did hens that qualified for only 2 or 3 years

Egg Production and Viability. From an analysis of viability data in the Suffolk laying trials in England from 1930 to 1935, inclusive, it was observed that, among the birds entered by 20 different poultry breeders, the birds entered by 12 poultry breeders had a viability of 93 per cent, whereas the birds entered by the other 8 poultry breeders had a viability of 80 per cent

Platt (1936) showed that among White Leghorns entered in the Vineland Egg Laying contests from 1918 to 1933, inclusive, the mortality during the first 3 years varied from 6 48 to 11 25 per cent, whereas

Fig 68   Average egg production and mortality during 48 weeks among pullets entered in laying trials from 1922 23 to 1936–37 at Harper Adams Agricultural College Newport Salop England   (Hutt, 1938a)

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Fig 68 Average egg production and mortality during 18 weeks among pullets entered in laying trials from 1922 23 to 1936 37 at Harper Adams Agricultural College Newport Salop England (Hutt, 1938a)

the shorter the life of the dam, the more liable was her progeny to have an excessive death rate and that the quality of the egg laid by dams has an effect on progeny viability. Munro (1936), Bird (1939), and Clark (1940) concluded that breeding for high egg production is compatible with breeding for viability. Hays (1949) observed that mortality rate by families during their first laying year showed practically no relation to egg production of survivors

The "Shaker" Fowl. A peculiar nervous disorder among the progeny of a Rhode Island Red male mated to distantly related females was reported by Scott, Morrill, Alberts, and Roberts (1950) Each female produced defective progeny The results of the mating consisted of 165 normal males, 78 normal females, and 89 "shaker" females

The original male was subsequently mated to White Leghorn females, 11 of which produced 27 normal males, 12 normal females, and 11 "shaker" females Out of 15 crossbred sires, secured from this second mating, mated to normal females, 5 carried the "shaker" gene and produced 34 normal males, 23 normal females, and 28 "shaker" females

The nervous disorder manifests itself by the eighteenth day of age, and accurate classification is possible by the fourth week The condition involves rapid movements of the head and neck and progressively increasing difficulty in walking without stumbling The condition is due to a loss of cerebellar Purkinge cells accompanied by a degeneration of those remaining The results secured from the different matings indicate that a sex-linked recessive gene is responsible for the condition

Another Sex-Linked Recessive Lethal. A peculiar nervous disorder among White Leghorn female chicks secured from one sire was described by Goodwin, Hutt, and Cole (1950) The disorder develops from as early as the third week to as late as the eighteenth week and is characterized by extreme listlessness followed by a complete coma, although some chicks exhibit great difficulty in breathing, which may or may not be accompanied by muscular spasms The results secured from matings involving the original sire with related and unrelated females, as well as matings involving some of his carrier and noncarrier sons, indicate definitely that the condition is due to a sex-linked recessive gene having lethal effects in females

Reduced Viability of Males Heterozygous for Sex-Linked Recessive Lethals. Stern and Novitski (1948) presented evidence indicating that viability is reduced in males carrying sex-linked recessive genes in a heterozygous state

"Jittery" Chicks. A nervous disorder of chicks manifested by a retraction of the head over the back and accompanied by a rapid shaking of the head was reported by Bohren (1950). The character proved to be highly lethal, only about 1 per cent of the females reaching maturity

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of mortality from the same causes Except for eight cases of lymphomatosis over a period of 7 years, no recognized infectious fatal diseases were encountered

The six inbred lines of Brown Leghorns differed among themselves in their resistance to various disorders In one inbred line, pathological conditions associated with the reproductive system caused 4 per cent mortality, whereas in two other inbred lines there was practically no mortality from this source and in another inbred line noted for high egg production the mortality due to reproductive disturbances was only 1 per cent Practically all cases of cannibalism appeared in one inbred line The results secured indicated to Greenwood the heritability of resistance to nonspecific disorders

Genetic Resistance to Avian Diphtheria. Apparently one of the first reports that provided evidence that relative resistance to a specific disease could be developed by breeding was submitted by Frateur (1924) In the case of avian diphtheria his rather meager results indicated that susceptibility was due to a single recessive gene

Genetic Resistance to "Blue-Comb" Disease This is primarily a pullet disease, since cockerels are rarely affected Most of the outbreaks occur about the time pullets are ready to lay or have commenced laying, especially if hot weather prevails at that time The amount of mortality varies considerably A disturbed physiological condition is involved Cole (1950) presented evidence that different strains of White Leghorns differed in degree of susceptibility to the disease and that there were significant differences between sire families within a strain Also the sires whose progenies were quite susceptible were closely related, for the most part The level of mortality in the progeny secured from crossing two strains that differed in degree of susceptibility was about half way between the level of mortality in the relatively resistant and the relatively susceptible strains

Genetic Resistance to Cecal Coccidiosis Rosenberg (1948) reported that relative resistance and relative susceptibility to *Eimeria tenella*, cecal coccidiosis in chickens, is hereditary Rosenberg McGibbon, and Herrick (1948) submitted additional evidence that substantiates the original observation Three trials were run of resistant × resistant matings and three trials were run of susceptible × susceptible matings The percentage of progeny that survived in each trial is given herewith

Matings	Trial 1	Trial 2	Trial 3
Relatively resistant × relatively resistant	52 7	45 5	44 3
Relatively susceptible × relatively susceptible	24 8	14 0	4 6

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The results of research to develop resistant strains by selection and breeding have been moderately successful. Roberts and Card (1926, 1935, 1936) were the first to report on the heritability of resistance to pullorum disease. The evidence upon which they concluded that resistance to pullorum disease is hereditary was as follows

1 Selection was effective in producing strains that were more resistant to infection than were unselected stocks

2 The selected stocks consistently maintained their relative resistance through successive generations

3 The F_1 generation produced by crossing resistant $\times$ susceptible stocks was as resistant as the resistant parents

4 Progeny of the above F_1 $\times$ resistant stock was significantly more resistant than was the progeny of the F_1 $\times$ susceptible stock

5 In the F_2 generation, susceptible and resistant strains were recovered by selection

6 The progeny of a susceptible male mated to susceptible females was much less resistant than was the progeny of the same male mated to resistant females

By both genetic and serological means, it was shown that acquired immunity had no bearing on the results secured

DeVolt, Quigley, and Byerly (1941), by appropriate subcutaneous inoculation tests, determined the degree of resistance of a strain of Rhode Island Reds that had been selected for over 12 years for progeny survival in the presence of natural infection. Also tested at the same time were the relatively resistant strains of White Leghorns that had been developed by Roberts and Card. Approximately 28 per cent of the Rhode Island Red chicks and about 33 per cent of the White Leghorn chicks survived as compared with 11 per cent survivors among chicks secured from breeding flocks that had been kept free of pullorum for several years previously

Roberts, Severens and Card (1939) concluded that the difference between resistant and susceptible chickens is due to an inherited differential in the number of lymphocytes at the time of greatest susceptibility, which is immediately after the chicks are hatched. Severens, Roberts, and Card (1944) observed that resistant chicks had larger spleens than those in susceptible chicks, the spleen being an important source of lymphocytes

Scholes (1942) and Scholes and Hutt (1942) concluded that differences in body temperature are responsible for differences in resistance to *S pullorum* rather than for differences in the number of lymphocytes in the blood, Hutt (1938a) and others having demonstrated that during the first 10 days after hatching body temperature rises relatively more

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panied by irregularity of pupils is frequently associated with ocular lymphomatosis

It should also be noted that Burmester (1945) observed that lymphomatosis occurs about twice as frequently in females as in males when the two sexes are exposed to infection under natural conditions Burmester and Nelson (1945) showed that male sex hormones secreted by the testes increase the degree of resistance to lymphomatosis in chickens, thus confirming the original observation of Marine and Rosen (1940, 1941)

Wilcke, Lee, and Murray (1938) concluded that it should be possible, by selection and breeding, to develop strains of birds relatively resistant or susceptible to fowl leukosis, and Lee and Wilcke (1939) added that the most important methods of controlling the disease included culling and the use of breeding stock from resistant strains

Hutt (1939) reported that, after 2 years of selection on the progeny-test basis with White Leghorns, a relatively resistant line and a susceptible line were established whose progenies differed significantly with respect to mortality from different types of the avian leukosis complex Next there followed a report by Hutt, Bruckner, and Cole (1939) dealing with the results secured from the third generation, and this in turn was followed by a fourth generation report by Hutt, Cole, and Bruckner (1941) In the fourth-selected generation, pullet mortality between 160 and 500 days of age was 38 per cent in the relatively resistant strain as compared with 64 per cent in the original unselected population The relatively resistant line had a pullet mortality of 12 per cent due to lymphomatosis and related types of the avian leukosis complex, whereas the susceptible line had a mortality of 26 per cent from similar causes

Blakemore and Dalling (1939) and Williams, Lampman, and Holm (1941), who practiced selection to reduce mortality but not to increase susceptibility, succeeded in reducing mortality apparently without increasing the inherent resistance to lymphomatosis

Jeffrey, Beaudette, and Hudson (1942) selected for resistance and susceptibility but observed a reduction in the incidence of lymphomatosis in both lines Taylor, Lerner, DeOme, and Beach (1943), carried on 8 years of progeny-test selection for resistance and susceptibility on the basis of mortality in females from 5 to 18 months of age They found that their line that was bred for relatively low incidence of mortality from lymphomatosis had about as much mortality as the original stock from which it was selected They also observed that the significant differences in mortality between their relatively resistant strain and their susceptible strain indicated differences in the herita-

panied by irregularity of pupils is frequently associated with ocular lymphomatosis

It should also be noted that Burmester (1945) observed that lymphomatosis occurs about twice as frequently in females as in males when the two sexes are exposed to infection under natural conditions Burmester and Nelson (1945) showed that male sex hormones secreted by the testes increase the degree of resistance to lymphomatosis in chickens, thus confirming the original observation of Marine and Rosen (1940, 1941)

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The environmental conditions under which chickens are reared may have considerable influence on the incidence of mortality from lymphomatosis Hutt, Cole, Ball, Bruckner, and Ball (1944) and Hutt, Cole, and Bruckner (1945) found that chickens raised in relatively close proximity to adult birds suffered much higher mortality than similar chickens reared at considerable distance from adult stock, the first 2 weeks of the rearing period being very important The Cornell University investigators developed two relatively resistant strains, C and K, the K resistant strain being superior to the C resistant strain There was simultaneously developed a C susceptible strain In Fig 70 are shown the effects of different degrees of exposure on total mortality and mortality from neoplasms, over 90 per cent of the mortality from neoplasms being due to lymphomatosis In Fig 70, A, B, C, and D represent chicks secured from four private breeders

In Fig 70 it is apparent that under conditions of mild and severe exposure, respectively, mortality from lymphomatosis was much less in the K resistant strain than in the C resistant strain and that these two strains were much superior to the C susceptible strain The A, B, C, and D strains were only moderately resistant The upright bars in Fig 70 indicate that there is a general relationship between mortality from neoplasms (90 per cent lymphomatosis) and total mortality, a fact which should be of considerable interest to poultry breeders

In the inbred lines of White Leghorns at the Regional Poultry Research Laboratory, Waters and Prickett (1946) observed that mortality due to visceral lymphomatosis was 24 4 per cent, as compared with 9 8 per cent due to the neural type, and 1 0 per cent due to the ocular type The visceral type appeared as early as 30 days of age, the neural type during the first 300 days of age, and the relatively few ocular cases after 120 days of age The different inbred lines varied with respect to age and relative severity of the different types of lymphomatosis Waters (1947) stated that the incidence of lymphomatosis is determined by the age of the chickens at the time they are exposed to the disease the severity of the exposure, and genetic resistance to the disease The inbred lines showed considerable variability with respect to resistance and susceptibility to lymphomatosis, but significant differences in mortality prevailed for the most part between the relatively resistant and the susceptible lines, as shown in Fig 71

The inbred lines at the Regional Poultry Research Laboratory, two of which are mentioned in Fig 71, had a coefficient of inbreeding of about 60 to 80 per cent In this respect, it is interesting to observe that mortality from lymphomatosis in resistant line 6 was maintained at a relatively low level from 1945 through 1947

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under conditions of natural exposure to the disease. From year to year, environmental conditions were kept as uniform as possible. Egg production, egg size, and body size were taken into consideration in selecting breeding stock. Figure 72 shows the extent to which the susceptible line became differentiated from the *C* resistant and the *K* resistant strains with respect to *percentage of mortality from neoplasms among female progeny between 42 and 500 days of age*

Fig. 72. Differentiation of lines relatively resistant or susceptible to neoplasms as a result of selective breeding during 11 years. The graphs are smoothed by using a 3-year moving average (except for terminal points). Hutt and Cole, 1948.)

In Fig. 72, the break in the graphs at 1942 indicates a difference in average severity of exposure to which the growing chickens were subjected each year. From 1935 to 1942, one-half of susceptible strain and one-half of each of the *C* resistant and *K* resistant strains were subjected to mild exposure, and the other half of each of these three lines to severe exposure. From 1942 to 1946, all the chickens in each of the three lines were subjected to severe exposure. It is interesting to note that mortality from neoplasms (90 per cent lymphomatosis) in the two resistant lines during 1944 and 1945 was about 5 to 8 per cent, whereas in the unselected population of 1935 mortality due to neoplasms was about 18 per cent.

A leukosis susceptible line (*S*) and a leukosis relatively resistant line (*R*), developed after 20 years of selective breeding, were crossed recipro-

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A leukosis susceptible line (*S*) and a leukosis relatively resistant line (*R*), developed after 20 years of selective breeding, were crossed recipro-

TABLE 7

PERCENTAGE OF VIABILITY OF CHICKS TO 24 WEEKS OF AGE IN NONINBRED,
INBRED, AND TOPCROSS MATINGS OF WHITE LEGHORNS

(Waters 1938)

Year	Noninbred	Family	Inbred	Topcross
1932–1937	84	{ All families	77	90
		{ Family 1	71	91
1935–1937	84	Family 2	69	85
1935–1936	82	Family 3	63	85
		{ Family 4	73	96
1936–1937	85	{ Family 6	89	91
		{ Family 7	83	88

The data given in Table 7 show that the viability of the chicks of the inbred matings was considerably lower than that of the noninbred matings but that the viability of the chicks of the topcross matings was higher than the viability of chicks of the noninbred matings

Dudley and Pease (1948) compared the viability of White Leghorn pullet progeny secured from outbred matings and from topcrossing matings Rearing-pullet viability from the outbred matings was 70 per cent and from the topcross matings 78 per cent, the laying-pullet viability from the outbred matings was 61 per cent and from the topcross matings 58 per cent In this particular case, outbreeding and topcrossing produced similar results

With respect to crossing inbred lines, Maw (1942) suggested that better results would probably be secured from topcross matings than from matings between inbred lines where some relationship exists between the lines Maw (1949) observed no significant differences in viability from 168 to 600 days of age among the pullet progenies secured from crossing inbred lines and from control matings

Crossbreeding Effects on Progeny Viability. Although comparatively few carefully controlled experiments have been conducted to determine the effects of crossbreeding on viability, broiler producers are interested in this problem because crossbreeding has usually been found to result in increased rate of growth during the first 10 or 12 weeks as compared with the purebred progenies of the parental breeds crossed

Two pure breeds in which the viability of chicks is high could not be expected to give materially higher viability when crossed, whereas two pure breeds in which the viability is comparatively low would be expected to give considerably higher viability when crossed, as the result of bringing together in the crossbred progeny favorable dominant genes from each of the purebred parents

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Crossbreeding was also shown by Ghostley and Nordskog (1951) to reduce progeny mortality Among eight strains representing Australorps, Barred Plymouth Rocks, New Hampshires, and Rhode Island Reds, matings were made within strains, between strains, and between breeds Progeny mortality to 8 weeks of age was as follows within strains, 29 per cent, between strains, 20 per cent, between breeds, 16 per cent Mortality during the first laying year was about 10 per cent less among the pullets secured from the strain and breed crosses than among the pullets secured from matings within strains

Mortality Reduced by Breeding Several investigators have reported results on experiments aimed at reducing mortality by selection and breeding It is obvious, of course, that genetic research involving mortality among growing chickens, laying pullets, and older females is much more complicated than research on embryonic mortality After chicks are hatched, the environmental conditions with which they have to contend for the rest of their lives are far more variable than during the period of incubation

Throughout their lives, birds are subjected to variable conditions of management, sometimes including faulty brooding and housing and dietary deficiencies of one kind or another Birds are also subject to functional disorders, as well as the ravages of parasites and diseases A program of selection and breeding to reduce mortality should be based on a complete absence of culling of the progeny, except in case of dire necessity Obviously, the elimination of undesirable birds at the time of selecting breeders each year is a necessity, the logical method of selecting prospective breeders being on the family basis A breeding program to reduce mortality should also include reasonable uniformity in rearing, housing, and feeding methods from year to year

Among some of the earliest programs of breeding the results of which demonstrated the possibility of reducing mortality by breeding were those of Taylor and Lerner (1938), Marble (1939), and Bearse, McClary, and Miller (1939) Bearse, McClary, and Miller (1939) showed that as the result of 8 years of breeding two strains of White Leghorns, the progeny of one strain was found to be more resistant to disease than the progeny of the other strain, the pullet-rearing mortality being 25 and 32 per cent, respectively

Sturkie (1943) carried on 5 years of selecting and breeding to reduce mortality in a flock of White Leghorns that must have been a notoriously poor flock or perhaps suffered from some kind of epidemic, since the unselected generation preceding the 5-year breeding program suffered a laying-flock mortality of 89 per cent with no culling during the first laying year The data, for each of the 5 years, pertinent to the pullet

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TABLE 9

MORTALITY OF PULLET PROGENY OF HIGH-MORTALITY AND LOW-MORTALITY
WHITE LEGHORN MATINGS, RESPECTIVELY

(Bostian and Dearstyne 1944)

Kind of Matings	Progeny Mortality, per cent		
	1939	1940	1941
High-mortality matings	34	31	28
Low-mortality matings	31	24	11

Bryant and Johnson (1944) and Bryant (1945, 1946), with White Leghorns, observed family differences with respect to relative resistance to particular diseases   Bryant (1945) showed that among females, the higher the mortality during the growing period up to 20 weeks of age, the higher the mortality during the laying period from 140 to 525 days of age   Bryant (1946) showed that two strains that had been developed for high mortality and low mortality, respectively, produced progeny that had a laying-pullet mortality of 30 and 17 per cent, respectively

The results discussed up to the present indicate that it is possible to reduce mortality by breeding, provided the breeders are selected on the progeny-test basis and enough families of sufficient size are available from which prospective breeders are selected   However, since egg production, egg size, hatchability, rate of growth, and other characters of economic importance must be considered by poultry breeders, it is apparent that progress in reducing mortality to quite a low level would probably be relatively slow

Breeding for Higher Viability.   Poultry breeders whose flocks are plagued with high mortality from whatever cause would welcome any suggestions concerning the possibility of reducing the level of mortality and keeping it within reasonable bounds from year to year   Except for sudden outbreaks of such diseases as fowl cholera and Newcastle disease, the evidence presented in this chapter definitely suggests that a well-planned selection and breeding program offers the best hope

The results secured by Taylor et al (1943) and Hutt and Cole (1947, 1948) showed that progress in breeding for resistance to lymphomatosis is possible while at the same time selecting for egg production and other characters of economic importance   Lush, Lamoreux, and Hazel (1948) showed that in the flock of White Leghorns whose records they analyzed there was a significant positive correlation between the heritability of resistance to leukosis and the heritability of resistance to other causes of death, and that resistance to total mortality was considerably more

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9 · Meat Production

The primary purpose of raising chickens and keeping layers is to convert feed into food of animal origin for human use. Since the cost of feed represents from one-half to over two-thirds of the total cost of raising chickens and producing eggs, it is obvious that any increased efficiency of feed utilization that can be brought about by breeding should be of great interest to poultry producers

Rapid growth, good body type, and superior breast fleshing are very desirable in chickens raised for meat production. How to improve chickens with respect to these three interrelated characters is discussed in this chapter

GROWTH

One of the most important factors affecting the efficiency of feed utilization in raising chickens is rate of growth. The faster that a chicken grows, the more efficiently is feed utilized during the growing period

Increase in body size involves an increase in the size of organs and muscle and in the growth of the bones of the body, this true growth being distinguished from the increase in size that results from the deposition of fat in the reserve tissue. True growth implies, therefore, an increase in water, protein, and mineral matter and involves an adequate supply of energy-producing nutrients, to support the various growth processes and vitamins of various kinds, which are essential for the attainment of physiological well-being and the most efficient utilization of feed

Environmental Conditions Affect Rate of Growth. Rate of growth is naturally affected by such environmental conditions as overcrowding, chilling or excessive heating during the brooding period, drafty brooder houses, improperly balanced diets, and parasites and disease. These facts are mentioned primarily for the purpose of emphasizing the importance of maintaining uniform conditions for different lots or groups of chickens that are being compared with respect to their inherent growth rates

Hays and Sanborn (1929) and Asmundson and Lerner (1933) observed that early-hatched chicks grew faster than late-hatched chicks. It is

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chicken increases in weight, the gain in weight which it makes per pound of feed consumed decreases This is because, as the chicken increases in weight, relatively more of the feed it consumes is used for maintenance Heuser (1946) pointed out that during the first 5 weeks of growth in White Leghorns the following percentages of the total feed consumed were used for maintenance first week, 65, second week, 70, third week, 80, fourth week, 85, fifth week, 90 For general-purpose chickens, these percentages would be somewhat higher This means that, as the chicken grows older and increases in weight, relatively less of the feed it consumes is used for growth These facts are in conformity with the law of diminishing increment Anyone interested in pursuing this matter further should consult Brody (1945) and Titus (1947)

Under ordinary conditions, the number of pounds of feed per pound of gain in weight increases as the chicken increases in weight or age That is why it is relatively more economical to produce broilers and fryers than roasters and capons If a sufficiently higher price per pound can be obtained for roasters and capons over broilers and fryers, the production of the former might be as profitable as the production of the latter

Efficiency of Feed Utilization Inherited. Evidence that efficiency of feed utilization is inherited was presented by Hess Byerly, and Jull (1941) Their least efficient Barred Plymouth Rocks required 21 per cent more feed per pound of gain in weight than their most efficient Barred Plymouth Rocks up to 8 weeks of age Crossbreds secured from crossing Barred Plymouth Rocks and New Hampshires, were observed to be relatively more efficient in utilizing feed than purebred progeny of the two parental breeds used in the cross McCartney and Jull (1948) observed differences in efficiency of feed utilization to 10 weeks of age between two strains of New Hampshires

Hess and Jull (1948) observed a heritable difference in feed utilization efficiency between individual chickens that could not be explained on the basis of body weight, rate of gain, or time Two Barred Plymouth Rock sires mated to similar females produced progenies that differed as much as 24 per cent in feed consumed by the time the birds were slightly over 1 pound in weight Purebred New Hampshire males consumed approximately 40 per cent less feed per pound of gain in weight than purebred New Hampshire females by the time both sexes weighed approximately 3 3 pounds At about 4 pounds, fast-growing males consumed 16 per cent less feed than slow-growing males By the time crossbreds and purebreds had attained about 2 25 pounds in weight, the crossbreds consumed 27 per cent less feed It was shown

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The hatchability percentages were as follows

Number of weeks on deficient diet	4	12	20	28	36
High hatchability group	88	85	83	92	66
Low-hatchability group	99	65	36	23	2

These data are extremely interesting and indicate clearly that great
variation existed among these hens in their ability to withstand a cer-
tain type of dietary deficiency

Strain Differences in Utilizing Riboflavin Riboflavin is a vitamin
that is necessary in adequate amounts for optimum growth of the

Fig 74 Left, chicken grown on a diet deficient in riboflavin   (Univ of Maryland)
Right, chicken grown on a diet deficient in thiamin   (Cornell Univ)

embryo and the chick Lamoreux and Hutt (1948) selected White
Leghorn breeders for resistance to riboflavin deficiency for five genera-
tions on the basis of their gains in weight made during the first 5 weeks
after hatching, the diet fed being deficient in riboflavin during the first
3 to 6 weeks The selection of breeders in a strain susceptible to ribo-
flavin deficiency was made from among surviving chickens that made
the least gains in weight to 3 weeks of age These chickens were then
given an adequate diet fortified with riboflavin supplements in order
to rear them to maturity A relatively resistant and a relatively suscep-
tible strain were thus established The results secured indicated that
the resistant and susceptible strains differed with respect to their ability
to live and grow on a diet deficient in riboflavin Lerner and Bird
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of cell multiplication during the development of the embryo account for differences in size of chick at hatching time   It has been well established by Byerly (1930) and others that during the latter part of the incubation period the embryos of general-purpose breeds are larger than the embryos of White Leghorns   Blunn and Gregory (1935) showed that, in White Leghorn and Rhode Island Red eggs of the same size, the Rhode Island Red embryos were relatively but not significantly larger than the White Leghorn embryos during most of the incubation period   Apparently, the slightly faster growth of the Rhode Island Red embryos was due to somewhat more rapid cell multiplication than in the White Leghorn embryos   Byerly, Helsel, and Quinn (1938) showed that, between embryos from reciprocal crosses of two breeds that differed considerably in mature body weight, the weight of the crossbred chicks was highly correlated with the size of the egg

Basing their findings on the fact that glutathione, which is involved in biological oxidation, stimulates cell multiplication, Gregory, Goss, and Asmundson (1935) and Gregory, Asmundson, and Goss (1936) demonstrated that glutathione values were correlated positively with the rate of cell multiplication at 14 days of incubation   It was also observed that the glutathione concentration in Barred Plymouth Rock embryos was slightly but consistently greater than in White Leghorn embryos from 5 to 19 days of incubation   Gregory, Goss, and Asmundson (1937) further observed that glutathione concentration was correlated with post-hatching growth rates and adult body weights

Chick Size in Relation to Egg Size. Several investigators, including Jull and Quinn (1925) and Hays and Sanborn (1929), have shown that at hatching time chicks weigh from 61 to 68 per cent of the weight of the eggs from which they hatch, part of the range in variation being due to the relative humidity maintained during incubation

Munro and Kosin (1940) demonstrated that at hatching time male chicks are slightly larger than female chicks and Kosin and Munro (1941) suggested that this difference was due in some measure to increased calcium utilization by male embryos during the last few days of the incubation period

Wiley (1950, I) reported that chick size was limited significantly by the space in the egg shell during the last 2 or 3 days of incubation

Early Growth in Relation to Chick Size   In growth-rate studies on Rhode Island Reds, Upp (1928) found that rate of growth was independent of chick size at hatching time   On the other hand, Halbersleben and Musselh (1922), Hays and Sanborn (1929) and Wiley (1950, II) observed that, during the first few weeks, small chicks at hatching time grew somewhat slower than large chicks hatched from the same dams

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Mixner, Reineke, and Turner (1944) found that 0 1 per cent of thiouracil in the drinking water of White Plymouth Rock chickens caused maximum thyroid enlargement Metabolic rate is lowered, the enlarged thyroid resulting from an increased secretion of thyrotropic hormone by the anterior pituitary, this increase being made possible because of the inhibiting effect which thiouracil has on the secretion of thyroxin by the thyroid gland El-Ibiary and Shaffner (1950) demonstrated that the capacity of the chicken to produce an enlarged thyroid gland is under genetic control

Schultze and Turner (1945) showed that, in White Leghorn and White Plymouth Rock growing chickens, there was a positive correlation between rate of growth and rate of thyroxin secretion up to the seventh and twelfth week, respectively, but a negative correlation between the two rates after those ages

Glazener and Jull (1946b) observed that feeding thiouracil at the 0 1 per cent level in the mash during the growing period depressed rate of growth Thyroid enlargement was relatively greater in the females than in the males Glazener, Shaffner, and Jull (1949) found that the level of thyroxin secretion was higher in a rapid-growing strain of New Hampshire females than in a slow-growing strain of New Hampshire females The difference in rate of thyroxin secretion between the two strains was less at 12 weeks than earlier El-Ibiary (1950) fed New Hampshire chicks a mash containing 0 2 per cent thiouracil and observed that growth was retarded as compared with untreated chicks, the difference in rates of growth being most noticeable between the second and the sixth weeks

Sex Differences in Growth Rate. The fact that males grow relatively faster than females has been demonstrated by several investigators (see Fig 76) Kempster and Parker (1936) compared the rates of growth of cockerels and pullets in White Leghorns, White Plymouth Rocks, and Rhode Island Reds, respectively The following data are pullet weights expressed as percentages of cockerel weights at 4-week periods

Age in weeks	0	4	8	12	16	20
White Leghorns	98	93	87	81	79	77
White Plymouth Rocks	99	93	89	80	82	78
Rhode Island Reds	99	98	92	86	85	81

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Glazener and Jull (1946b) observed that feeding thiouracil at the 0 1 per cent level in the mash during the growing period depressed rate of growth Thyroid enlargement was relatively greater in the females than in the males Glazener, Shaffner, and Jull (1949) found that the level of thyroxin secretion was higher in a rapid-growing strain of New Hampshire females than in a slow-growing strain of New Hampshire females The difference in rate of thyroxin secretion between the two strains was less at 12 weeks than earlier El-Ibiary (1950) fed New Hampshire chicks a mash containing 0 2 per cent thiouracil and observed that growth was retarded as compared with untreated chicks, the difference in rates of growth being most noticeable between the second and the sixth weeks

Sex Differences in Growth Rate. The fact that males grow relatively faster than females has been demonstrated by several investigators (see Fig 76) Kempster and Parker (1936) compared the rates of growth of cockerels and pullets in White Leghorns, White Plymouth Rocks, and Rhode Island Reds, respectively The following data are pullet weights expressed as percentages of cockerel weights at 4-week periods

Age in weeks	0	4	8	12	16	20
White Leghorns	98	93	87	81	79	77
White Plymouth Rocks	99	93	89	80	82	78
Rhode Island Reds	99	98	92	86	85	81

During recent years, the problem of developing rapid-growing strains of chickens has become increasingly important, largely as a result of

Fig 77 Left, showing for both sexes more rapid rate of growth in Rhode Island Reds and White Plymouth Rocks than in White Leghorns (Graph made from data of Kempster and Parker, 1936) Right, showing differences in growth rates of two strains of White Leghorns (Graph made from data of Waters and Bywaters, 1943)

the expansion of the commercial broiler industry Many private breeders have developed strains whose 10-week and 12-week average weights far exceed those usually obtained With respect to White Leghorns, kept primarily for market egg production, rapid growth is

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TABLE 10

AVERAGE WEIGHT IN POUNDS OF PUREBRED AND CROSSBRED PROGENIES AT 16 WEEKS OF AGE

(Henderson 1949)

	Males	Females
White Leghorn purebreds	2 9	2 3
Dark Cornish purebreds	2 7	2 2
Dark Cornish ♂ × White Leghorn ♀ crossbreds	2 9	2 2
White Leghorn ♂ × Dark Cornish ♀ crossbreds	3 0	2 5

crossbreds from the reciprocal cross weighed very little more than the White Leghorn purebreds

The data given in Table 11 pertain to crossbred matings such as are used in the commercial production of "broiler" chicks

TABLE 11

AVERAGE WEIGHT IN POUNDS OF PUREBRED AND CROSSBRED PROGENIES AT 12 WEEKS OF AGE

(Smith and Wiley 1950)

	Males	Females
White Wyandotte purebreds	3 7	2 8
Rhode Island Red purebreds	2 8	2 4
White Wyandotte ♂ × Rhode Island Red ♀ crossbreds	3 8	3 0
New Hampshire purebreds	3 8	2 9
Barred Plymouth Rock purebreds	3 3	2 6
Barred Plymouth Rock ♂ × New Hampshire ♀ crossbreds	3 7	3 1
New Hampshire purebreds	3 5	2 8
Barred Plymouth Rock purebreds	3 2	2 5
New Hampshire ♂ × Barred Plymouth Rock ♀ crossbreds	3 4	2 7
Barred Plymouth Rock purebreds	2 5	2 2
New Hampshire purebreds	3 0	2 5
Barred Plymouth Rock ♂ × New Hampshire ♀ crossbreds	3 7	2 9

The data in Table 11 show that the crossbreds secured from White Wyandotte ♂ × Rhode Island Red ♀ were slightly heavier at 12 weeks than the White Wyandotte purebreds, and considerably heavier than the Rhode Island Red purebreds, this particular strain of Rhode Island Reds apparently not being a rapid growing strain

The results of other matings given in Table 11 show that the Barred Plymouth Rock strains used were slower growing strains than the New Hampshire strains and that the crossbreds more nearly approached the purebred New Hampshires than the purebred Barred Plymouth Rocks

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observed that the growth of long bones in the body of males exceeds that of females by as much as from 13 to 16 per cent In bantams and other breeds, sex dimorphism in skeletal growth is greatest with respect to the shank (tarsometatarsus)

The longest bone of the leg (tibiotarsus) is laid down before the tarsometatarsus, but the latter grows faster Shank length, therefore, during different periods of growth, has been used by several investigators as an index of rate of body growth in all breeds of chickens Quisenberry, Roberts, and Card (1941) suggested that studies on skeletal dimensions should include diameters as well as lengths of bones, but it is doubtful that much would be gained by such a procedure Moreover, it would not be a practical method for poultry breeders to employ

Shank Length and Rate of Body Growth. Lerner (1937a, 1937b) and Jaap (1938) observed that shank length serves as a reliable index of body weight during most of the growing period and that shank length and body weight are more closely correlated during various growing periods than after the birds have attained mature body weight

Landauer (1934) pointed out that the relatively short shanks of the Creeper fowl are due to genes that bring about a retardation in the growth of the leg bones

A J G Maw (1935) found that the F_1 females secured from reciprocal crosses between Light Brahmas and Golden Sebright Bantams differed widely in the lengths of the leg and wing bones The two breeds also differed significantly in shape of skull

Jaap and Penquite (1938) observed that skeletal growth in chickens ceases earlier than does the growth of the body as a whole, rate of bone growth increasing from 4 to 15 weeks of age and decreasing relatively from 12 to 20 weeks of age with respect to body weight Jaap (1941) pointed out that the shanks of chickens attain their maximum length between 18 and 24 weeks of age, shank growth ceasing in females at about 5 months of age and in males at about 6 months of age Lerner (1943, 1944, 1946), employing progeny testing and sister selection on the basis of shank length, developed two lines of White Leghorns that differed genetically with respect to size as measured by shank length Lerner (1944) pointed out that the cumulative differences in postembryonic growth were mainly responsible for the shank-length differences between the relatively large-size line and the smaller-size line Lerner and Gunns (1944) found that the relatively large-size line had somewhat larger eggs than the smaller-size line

From a random sample of New Hampshire cockerels 12 weeks of age, Hull, Phillips and Williams (1943) selected three groups differing in shank length The group with the intermediate shank length was

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Fig 78 Showing the distribution of body weights in the parental or P_1, the F_1, and the F_2 generations, respectively, in matings between Barred Plymouth Rock males and Black Rose Comb Bantam females (Jull and Quinn, 1931)

Fig 79 Showing the distribution of body weights in the parental or P_1 the F_1 and the F_2 generations respectively, in matings between Black Rose-Comb Bantam males and Barred Plymouth Rock females (Jull and Quinn, 1931)

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future breeding purposes should be selected at about 4 to 6 weeks and again at 10 to 12 weeks of age.

FLESHING

The various classes of chickens include broilers, fryers, roasters, capons, and fowl. Within each class considerable variability in body shape and degree of fleshing is usually evident when the birds are dressed for market. Broilers, or roasters, or any other class of market poultry belonging to the same breed often exhibit considerable variability with respect to degree of fleshing.

Maw and Maw (1935) presented evidence indicating that the live bird outline is of some value in selecting breeding stock to produce well-proportioned and well-fleshed roasters. Maw and Maw (1938), by X-ray photographs of three Barred Plymouth males and their sons, showed that the body type of the sire has a considerable influence in determining the body type of his progeny The three sires significantly influenced the length of back, keel, and shank in their progenies. Maw and Maw (1939) reported that increase in body length and depth and increase in length of leg was inversely correlated with percentage of edible meat. On the other hand, length of keel and circumference of the tibiotarsus were positively correlated with percentage of edible meat.

Lerner (1937b) concluded that the growth of the breast muscle (pectoralis major) and of the leg bones in relation to the growth of body followed a similar course in Barred Plymouth Rocks and Black Minorcas

Jaap and Penquite (1938) reported that differences in body conformation of live birds could be determined quite accurately by comparing body weight, shank length, keel length, and anterior body depth. They also reported that the most desirable index of body shape in live birds is the relationship between shank length and cube root of body weight Lerner (1939), however, maintained that shank length was a better index of body proportions.

Jaap and Thompson (1940) observed that the sire's body shape is transmitted to his progeny to a high degree In their studies on heritable differences in adult female body conformation, they were not able to demonstrate any consistent relation between proportional length of shank and keel and proportional body depth. The shape, as well as the location of the keel in its longitudinal axis, were found to have more influence on the conformation of dressed birds than the length of the keel. Jaap (1941) found that differences in body conformation of various breeds became apparent at 12 weeks of age His Dark Cornish

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well-fleshed bird might have a poor appearance as a dressed bird because of relatively great depth of body Also, a shallow-bodied bird might be quite plump in appearance but actually have relatively less flesh than the deep-bodied bird For that reason, Bird maintained that body depth should be taken into consideration in relation to degree of breast fleshing S Bird (1948) established the fact that thickness of breast muscle, or roundness (plumpness) of breast, "is a character separate and independent of skeletal width of the thoracic cavity " He demonstrated that plumpness of breast in chickens is negatively correlated to depth but that since breast plumpness is apparently inherited from the male it should be possible to develop strains of plump-breasted, deep-bodied, fast-growing chickens by progeny testing

Frischknecht and Jull (1946) observed that their strain of New Hampshires was superior to their strain of Barred Plymouth Rocks in transmitting plumpness of breast to their progeny Crossbreeding Dark Cornish males and New Hampshire and Barred Plymouth Rock females produced a higher percentage of grade A birds than was secured from purebred matings Also, the fastest-growing chickens tended to grade the highest

Body weight, shank length, keel length, and breast width in relation to grade were determined by Lerner, Asmundson, and Cruden (1947) in New Hampshire cockerels and pullets, respectively, at 12 weeks of age, these birds being the descendants of a strain that had been bred for several years for improvement in meat quality The pertinent data are given herewith, body weight is given in pounds, and shank, keel and breast measurements are in centimeters

Grade	Males				Females			
	A+	A	B	C	A+	A	B	C
Body weight	4 14	3 82	3 12	3 01	3 64	3 44	2 68	2 63
Shank length	11 9	11 5	10 8	10 6	10 6	10 3	9 7	9 6
Keel length	10 4	9 9	9 4	9 2	9 8	9 3	8 8	7 5
Breast width	2 30	2 31	2 21	2 16	2 40	2 30	2 21	2 16

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estrogen-fattened birds may be prevented or remedied by rubbing a synthetic drug having androgenic effects on the combs and wattles

Among the numerous investigators who have conducted experiments in this field are Lorenz (1943, 1945a, 1945b), Jaap and Thayer (1944), Jaap and Thompson (1945), Thayer, Jaap, and Penquite (1944), and Sturkie (1946a, 1946b)

The effects on fattening and the grade of dressed birds by adding thiouracil, a thyroid depressant, to the diet have been investigated by Kempster and Turner (1945), Glazener and Jull (1946b), Andrews and Bohren (1947), Moreng and Shaffner (1949), Detwiler, Andrews, and Bohren (1950), and others

Conclusion   The discussion in the preceding pages of this chapter has emphasized the importance of breeding for rapid growth in order that chickens utilize feed as efficiently as possible   This is very important because under normal times the cost of feed constitutes about 50 per cent of the total cost of raising chickens and in abnormal times as much as 70 per cent   In developing rapid growing strains of chickens the real objective is to increase efficiency of feed utilization

The phenotypic selection of future breeding stock should be quite effective in a selection and breeding program to develop rapid growing strains   The period of from 4 to 6 weeks is apparently a good time to make the first selection of future breeders   the fastest growing birds being wingbanded   The second selection should be made at 10 to 12 weeks and certainly before any of the cockerels are sold   During each of these two selection periods, length of shank would probably be the best criterion, although it is possible that body weight would serve almost as well and would be a time saving method   Although phenotypic selection would be relatively effective, consideration of family averages of body weight would be more effective

It is hardly necessary to point out at this time that reasonably good sized families are very desirable, and a relatively large number of single-male pen matings should be maintained each year   Both of these stipulations are necessary to permit intense selection of future breeders since many genes determine rate of growth, body type, and fleshing ability

Since it has been shown that there are maternal effects upon body weight, the selection of future breeding females is quite important   Since it has also been shown that the sire transmits body type to his progeny to a high degree, it is necessary to give greater consideration to the selection of future breeding males than females   Moreover the average sire has about ten times as many progeny as the average dam   That is why it is so important to test as many sires as possible each

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10 · Egg Production

The principal objective in breeding for high egg production is to increase the efficiency of the laying stock in the utilization of feed, since feed cost amounts to over one-half or usually about two-thirds of the total cost of producing eggs

During 1945 to 1947, the average annual gross income obtained from eggs, farm-raised chickens, and commercial broilers in the United States was $2,955,284,000. Eggs contributed 62 5 per cent of this income; farm-raised chickens contributed 27.8 per cent; commercial broilers contributed 9.7 per cent. It is evident, therefore, that egg production is the major interest of most farmers and commercial poultrymen As a matter of fact, the income obtained from farm-raised chickens results largely from the sales of surplus cockerels and unwanted pullets from flocks raised primarily for laying-flock replacement purposes.

Maintenance Requirements. Feed consumed by layers is used for maintenance, for any increase in body weight that may occur, and for egg production. By far most of the feed that layers consume is used for maintenance. Large birds use relatively more of their feed for maintenance than small birds. Of two birds of the same size and laying the same number of eggs, the one laying the larger eggs consumes slightly more feed than the other.

Joshi, Shaffner, and Jull (1949), in a study involving New Hampshire laying pullets, observed that when these birds were laying at the rate of 72 per cent, approximately 71 per cent of the feed they consumed was used for maintenance, 2 per cent for increase in body weight, and 27 per cent for the production of eggs.

Birds that lay no eggs yield no profits to the poultry producer because all the feed consumed is used for maintenance That is why regular culling of the laying flock is desirable. Unprofitable producers, if in good physical condition, should be sold for their meat value, thus reducing cost of feeding the flock.

The rate of egg production is the most important factor that influences the feed cost of producing eggs. Since maintenance requirements increase in proportion to increase in body size, many people entering the business of producing market or hatching eggs want to know whether

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TABLE 13

POUNDS OF FEED REQUIRED TO PRODUCE 1 DOZEN 2 OUNCE EGGS BY BIRDS, WITHOUT GAIN OR LOSS IN WEIGHT, LAYING AT SPECIFIED RATES

(Byerly 1941)

Eggs per 100 Birds per Day	Average Body Weight, pounds				
	3	*4*	*5*	*6*	*7*
10	17 0	20 3	23 2	25 9	28 4
20	9 4	11 0	12 4	13 8	15 1
30	6 8	7 9	8 9	9 8	10 6
40	5 6	6 4	7 1	7 8	8 4
50	4 8	5 4	6 0	6 6	7 1
60	4 3	4 8	5 3	5 7	6 2
70	3 9	4 4	4 8	5 2	5 5
80	3 6	4 0	4 4	4 7	5 1
90	3 4	3 8	4 1	4 4	4 7*
100	3 2	3 6	3 9	4 1	4 4

allowed different amounts of feed The first group was allowed free access to the feed at all times, and records were kept of the amount of feed consumed each day The second group was given 87 5 per cent as much feed as that consumed by the first group the preceding day The third group was given 75 per cent as much feed as that consumed by the first group the preceding day Egg production of the second group was 68 2 per cent of that of the first group, and egg production of the third group was 47 5 per cent of that of the first group In other words, the decrease in egg production of the second and third groups was a little more than twice as much as the decrease in feed intake

Readers who may be interested in further observations on the gross and net efficiency of egg production as influenced by body weight and level of production should consult Almquist (1944), Brody (1945) Brody, Funk, and Kempster (1938), Loosli (1947), and Maynard (1946)

Yearly Rate of Lay. From 1924 to 1948, the trend in rate of lay showed a perceptible upward trend, except during the period of economic depression in the early thirties (see Fig 81) This steady increase in rate of lay resulted from securing more early-hatched chicks, more efficient laying-flock management, better-balanced diets, flocks containing a higher percentage of pullets, improvement in the "bred-to-lay" quality of the laying flocks, and other factors Poultry breeders like to think that the major influence determining the increased rate of lay which has taken place has resulted from the selection and progeny testing that has been carried on for many years to develop superior laying strains It should be kept in mind, however, that environmental

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ENVIRONMENTAL FACTORS AFFECTING EGG PRODUCTION

There are several environmental factors that affect rate of lay and the total number of eggs produced by a flock during the laying year. Poultry breeders can ill afford not to keep these factors in mind in attempting to appraise the relative laying ability of succeeding generations of pullets produced during a long-time breeding program. This is particularly true when the time comes to select future breeders from among the families of full-brothers and full-sisters produced each year.

Date of Hatch. With respect to commercial broiler production, chicks are hatched the year round so that date of hatch is not of particular concern. With respect to market egg production, however, the approximate date or season of the year when chicks are hatched is of some importance. Each year by far most of the chicks secured for laying-flock replacements are purchased during February through May. Since White Leghorn females have a lower adult body weight than general-purpose females, White Leghorn pullets attain sexual maturity and mature body weight relatively sooner than general-purpose pullets and therefore can be purchased from 2 to 4 weeks later than the latter and still start to lay about the same time.

In some cases, chicks hatched during January and February may start laying during July or August and, after laying for a few weeks, undergo a partial neck molt. On the other hand, in southern sections of the United States, chicks hatched during June and later may be retarded in growth because of excessive heat, as pointed out in Chapter 9.

The point of this discussion is that the pedigree poultry breeder should hatch his chicks each year at a time that will permit the proper evaluation of families of full-sisters and families of half-sisters with respect to age at sexual maturity and first-year egg production.

Location and Management. Gutteridge and O'Neil (1942) reported that egg production was influenced by environment to a greater extent than by heredity in the case of three strains of pullets of the same breed kept at each of three widely scattered locations. The strains were designated *A*, *B*, and *C*, respectively, and the locations

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that the time of laying is influenced by the activity of the birds during the feeding period irrespective of the lighting periods employed (Fraps, Neher, and Rothchild 1947)

Since artificial lighting is so universally practiced, the poultry breeder should treat all full-sister families and all half-sister families on a comparable basis for the proper appraisal of family averages

According to Dobie, Carver, and Roberts (1946), providing artificial lighting in the laying house during the fall and winter months to give the birds a 13-hour working day tends to increase the fall and early winter egg production of pullets Riley and Byerly (1943) demonstrated the effectiveness of a 14-hour lighting period in maintaining good egg production among yearling hens For best results, pullets of different ages should be kept in separate pens and the yearlings should be kept by themselves

Light is usually provided by 40-watt Mazda lamps Each lamp will provide sufficient lighting for about 200 square feet of floor space, in a long laying house the lamps are spaced about 10 feet apart The lamps are located about 6 feet above the floor and are arranged to shine on the roosting quarters in order to encourage the birds to leave the roosts when the lights come on in the morning

The lighting system most widely used consists in using morning lights only, because it is simpler and at dusk the day's work is done Also, no dimming system is necessary It is very important to give the birds practically the same amount of artificial light and daylight from day to day Failure to turn the lights on a few mornings may cause a drop in egg production

Artificial Lighting for Pullets When laying pullets are placed in the laying house in the fall of the year, they are still in a growing condition Giving them a 13-hour day by means of artificial lights in the morning stimulates egg production Feed consumption is increased, so that they keep on growing and laying well at the same time Morning artificial lighting should be continued until about April 1 Feed and water should be available for the birds when the lights are automatically turned on early in the morning In cold climates the water should be kept from freezing by the use of water heaters

Artificial Lighting for Yearlings During July and August egg production is likely to drop considerably Some hens start to molt and others also tend to lose body weight and stop laying Beginning about July 1, it is a good practice to cull the flock thoroughly Care must be taken to prevent the birds from slackening in their feed consumption and thus losing body weight By using artificial lighting combined

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research is necessary before it can be demonstrated that the feeding of thyroprotein is a practical means of increasing egg production

Treating White Leghorns in their first year of egg production with thiouracil and thyroxine, led Booker and Sturkie (1950) to conclude that the rate of thyroxine secretion differed between birds that laid at the rate of two eggs per clutch and birds at the rate of four eggs per clutch

PHYSIOLOGICAL FACTORS RELATED TO EGG PRODUCTION

There are certain physiological factors related to egg production to which some attention must be given by the poultry breeder to enable him to make the most efficient selection of breeding stock each year

Body Size It has been pointed out previously that size of bird is of economic importance in egg production, since the larger the bird the greater the amount of feed consumed for body maintenance On the other hand, the salvage value of the larger bird is greater when egg production ceases Also, good body size is important in breeding flocks kept for the production of eggs that are to be hatched into "broiler chicks

Among flocks that have not been bred especially for high egg production, there is a tendency for the largest birds to lay relatively the fewest eggs On the other hand, in flocks that have been bred for high egg production and where selection for body size has been practiced in the breeding program there appears to be little correlation between body size and egg production Atwood and Clark (1930) and Bryant and Stephenson (1945), among others, observed little or no relationship between body size and egg production On the other hand, Hays (1939) submitted evidence showing that in some strains of different breeds there was a negative correlation between body size and egg production Also, Quisenberry, Roberts, and Card (1941) who made reciprocal crosses between Dark Cornish and White Leghorns secured results in the F_2 generation indicating linkage between factors for body size and egg production There was a significant negative correlation $(-0\,36)$ between body size and egg production

Culling to Maintain Efficient Level of Production Certain physical characters can be used to distinguish birds which are in laying condition from those which are not laying and certain physiological changes that take place in relation to egg production make it possible to distinguish the best layers from the poorest ones if observations are made at sufficient intervals Although the selection of prospective

research is necessary before it can be demonstrated that the feeding of thyroprotein is a practical means of increasing egg production

Treating White Leghorns in their first year of egg production with thiouracil and thyroxine, led Booker and Sturkie (1950) to conclude that the rate of thyroxine secretion differed between birds that laid at the rate of two eggs per clutch and birds at the rate of four eggs per clutch

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ment in the beak, shanks, toes, vent, and eye ring and in the white of the ear lobe of breeds having normally white ear lobes. The yellow pigment comes from the feed which the birds eat. When a pullet starts to lay, the yellow pigment of the feed is diverted to the yolks of the eggs instead of going to the beak, shanks, and other parts noted previously. As long as egg production continues, these parts gradually lose their pigment, so that they become bleached in appearance (see Table 14). The longer a bird continues to lay, the greater the degree of bleaching. The yellow pigment does not return to the beak, shanks, and other parts until production ceases.

TABLE 14

AVERAGE ANNUAL EGG PRODUCTION OF GROUPS OF WHITE LEGHORN HENS SELECTED
ON THE BASIS OF VENT, BEAK, AND SHANK COLOR

(Blakeslee Harris Warner and Kirkpatrick 1917)

	Number of Birds and Mean Annual Production					
	Vent		Beak		Shanks	
Color Class	Birds	Production	Birds	Production	Birds	Production
Pale	101	190	114	184	141	170
Medium	91	152	80	163	104	161
Yellow	183	136	181	132	130	123
Entire flock	375	155	375	155	375	155

The order in which the pigment disappears from the different parts is as follows: (1) from the vent, (2) from the eye ring which is formed by the inner edges of the eyelid, (3) from the ear lobes of breeds having white ear lobes, such as Leghorns, (4) from the beak, beginning at the base and extending toward the tip, (5) from the shanks, disappearing first from the front of the shank and later from the rear.

Under average conditions, a completely bleached beak indicates that the hen has been laying for 4 to 6 weeks whereas completely bleached shanks indicate that the hen has been laying for 20 to 24 weeks.

It should be kept in mind that the degree of depigmentation at any particular time is not an index of the length of the laying year. This fact was established by Warner (1942) in White Leghorn pullets.

Time and Duration of Molt. Under normal conditions the average living bird usually undergoes her first complete annual molt at the conclusion of her first year of laying. The time and duration of the first annual molt are important points in distinguishing between poor and good layers. Birds that molt early are usually the poorest layers. The bird that is a poor layer usually stops laying in July or August

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feathers in each wing, and, when the complete body molt begins, the first primary to be dropped is the inner one next to the axial feather (see Fig 83)

In the case of the early molter, 2 weeks after the first primary is dropped, the second one, next to the axial feather, is shed, and at 2-week

Fig 83 Wing of a Barred Plymouth Rock showing ten primary feathers which are separated from the secondary feathers by the short axial feather marked X (R I Phillips Univ of Maryland)

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Fig 83   Wing of a Barred Plymouth Rock showing ten primary feathers which are separated from the secondary feathers by the short axial feather marked X   (R I Phillips Univ of Maryland)

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Greenwood (1936) made the interesting observation that as long as the ovary and oviduct remain functionally active the process of molting

FIG 85 Wing of a fast molting bird To the left of the axial feather (X) five primary feathers shed at about the same time are being replaced (R J Phillips Univ of Maryland)

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TABLE 16

MORTALITY AND EGG PRODUCTION RECORDS OF THE WHITE LEGHORN PROGENY
OF EACH OF TWELVE SIRES

(Lerner and Taylor 1940a)

Sire	Daughters Housed number	Mortality among Daughters per cent	Hen Housed Average Egg Production number	Survivors Average Egg Production number
G14	87	25	178	214
G36	79	56	93	152
G52	62	27	190	225
H8	61	36	158	203
H33	52	21	163	191
H42	56	61	114	193
H43	60	38	135	180
H46	68	60	111	190
H62	66	30	178	227
H79	99	24	169	193
H90	95	26	166	197
H91	61	41	154	204

and the amount of culling should be taken into consideration in attempting to appraise the real breeding worth of sires and dams. Also, if a production index is used from year to year as a measure of family average egg production, poultry breeders must keep in mind that, since the amount of mortality affects the production index, any year showing excessive mortality may lead to a distorted appraisal of the results.

Lerner and Taylor (1940a) concluded that controlled culling not only results in some economy of feed cost in producing eggs but also salvages the market meat value of those birds that are culled while still in good physical condition but would probably have died before the end of the first laying year. Furthermore, controlled culling of sire families during the first laying year at levels of 12 to 24 per cent makes possible the ranking of the sires according to their relative merits.

Bird and Sinclair (1938) observed that culling the poorest livers up to 25 per cent of each sire's family still permitted the proper ranking of the sires and their progenies. All sire families should be culled at approximately the same level. Nevertheless, there must be some limit to the extent of culling practiced especially since mortality usually removes a considerable number or there will be too few survivors of a family at the end of the first laying year. This is particularly important in the case of the daughters of each dam. Bird and Sinclair suggested ' that the chances for a male to qualify as a truly superior breeding sire

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(1927a), Atwood (1929), and Heywang (1938). Egg production, barring disease, normally follows a definite rhythm, the interval in hours between the laying of eggs on consecutive days depending upon the size of the clutch. There is a regular trend of reduced time intervals between layings in a clutch as the clutch size increases. Heywang observed that, although the time sequence in the laying of successive eggs in clutches follows a regular trend, exceptions sometimes occur among birds that lay small or large clutches Hays (1936c, 1938), among others, observed that the shortest time intervals between layings within clutches were characteristic of birds laying large clutches. Also, the larger the clutch size, usually the shorter the interval between clutches and the higher the annual egg production. It is obvious, therefore, that clutch size constitutes a sound measure of laying ability.

No Cycles of Production. In a number of cases in the early studies on the inheritance of egg production it was customary to divide first-year egg production into four rather arbitrary periods: winter, spring, summer, and fall. Eggs laid during these periods were called "cycles of production." The interesting observations of Pearl (1915a, 1915b) and Pearl and Surface (1911) in their extensive analyses of egg-production records in Barred Plymouth Rocks at the Maine Experiment Station were largely responsible for the adoption of so-called "winter cycle" as a criterion of inherent laying capacity among birds. Before the time of their investigations it was rather unusual for birds in the United States to lay many eggs during the winter months, and, since they found that the best winter layers were usually the best annual layers also, they concluded that the winter cycle of production, from the first of November to the last of February, was of considerable significance in determining the inherent laying capacity of a bird A cycle of production was defined by Goodale (1918a) as a period of production alternating with a period of decreased production or cessation of production. It should be observed at this time, however, that these so-called cycles of production were purely arbitrary designations.

Moreover, after a comprehensive study of records of production in White Leghorns at the Utah Experiment Station, reported by Ball, Turpin, and Alder (1914) and by Ball, Alder, and Egbert (1916), Ball and Alder (1917) were led to believe that the winter cycle does not represent correctly a biological entity. They also stated that a record of production of 3 years is a safer guide than the record for the pullet year only in determining the inherent laying ability of a bird Goodale (1918b) found no evidence of the existence of a winter cycle among Rhode Island Reds at the Massachusetts Experiment Station Brody (1921), from an analysis of the first year of production of 1210 Barred

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molt Hays (1943) observed that in the Massachusetts Experiment Station flock of Rhode Island Reds the biological laying year averaged 377 days, 12 days longer than the calendar laying year of 365 days from commencement of laying From the standpoint of record keeping, it is much simpler to determine first-year egg production on a calendar basis, this being the customary basis used by practically all poultry breeders

For many years the trapnest has been employed as a means of determining the number of eggs laid by the members of a flock Cook (1937) reported that in 1869 the United States patent office issued a patent to D P Leich for a trapnest although this nest was apparently not practical In 1899 a patent was issued to George I Lytle for a trapnest that apparently was practical However, trapnesting was probably carried on by a limited number of poultry breeders before that time

In the early days of trapnesting, many poultry breeders considered it very important to determine the exact numbers of eggs laid by each member of the flock Trapnesting a flock of layers throughout the first laying year is laborious, time consuming, and expensive Moreover, except for publicity purposes in the event of a phenomenal record, the exact number of eggs a bird lays during her first laying year has relatively little significance in determining her breeding worth Hervey (1923) secured the following results with White Leghorns

Range in egg production of dams	201–230	231–260	261–290
Average egg production of daughters	170	187	213

Jull (1934a, 1934b) and Hays (1946a) concluded that the dam's first-year record of egg production could not be used as a criterion of her breeding ability Hays secured the following results with Rhode Island Reds that for several years had been bred for high egg production

Range in egg production of dams	180 219	220 259	260 299	300 330
Average egg production of daughters	190	211	220	228

Hervey (1923), Munro Bird, and Hopkins (1937) and Hays (1946a) reported correlations of 0 057, 0 152 and 0 159 respectively between the first-year egg production of dams and their daughters These correlation values and the data of Hervey and Hays indicate that within a rather wide range of egg production the dam's record is not a reliable index of her breeding ability Hays (1919) suggested that dams varying as much as about 40 eggs could be expected to produce daughters with similar egg-production records The particular point of interest

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per month and pointed out that size of family, full sisters or half-sisters, was a factor to be considered

Numerous poultry breeders participating in the record of performance stages of the National Poultry Improvement Plan trapnest their birds 3 days per week, this method having been found to be sufficiently reliable, especially with respect to determining the average egg production per family   Trapping 3 days each week makes possible the trapping of twice as many birds with the same amount of labor as with trapping 6 or 7 days a week, more families from more matings could be tested, and a more intensive selection program could be carried on, which in turn should lead to more rapid progress in developing high-laying strains

A 300-Day Trapnest Year.   Trapnesting birds for the entire first laying year from commencement of laying means that many of these birds still occupy the laying house or breeding pen from August to December   In many cases family-average egg-production records cannot be computed until some members of numerous families of full-sisters complete their first laying year in October or later   This is long after the new crop of pullets should be housed   In order to give poultry breeders an opportunity to clean and disinfect the laying houses and breeding pens in plenty of time for the new crop of pullets, a 300 day trapnest year is employed instead of a 365 day trapnest year

The 500-Day Test.   Hutt (1949) has found the 500 day test to be very satisfactory in carrying on his extensive breeding program at Cornell University   Egg production records include the eggs laid from commencement of laying to 500 days of age for each bird   Since chicks are hatched at weekly intervals during the normal breeding season this method makes it possible to discontinue trapping the layers at weekly intervals as they reach 500 days of age   In this way, laying houses and breeding pens can be made ready in ample time to house the new crop of pullets at weekly or less frequent intervals if such is deemed desirable

YEARLY DECLINE IN EGG PRODUCTION

Although a few hens have been known to lay more eggs in their second laying year than in their first laying year, in by far most of the cases there is a decline in egg production with each succeeding year   The yearly decline in egg production is of economic importance to egg producers, because it is related to the problem of deciding how many of the best first-year layers should be kept for the second laying year   It has long been the custom of many egg producers to maintain flocks

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In Fig 87, data by Insko, Steele, and Wightman (1947) are given pertaining to the average egg-production records for each of 3 years for a selected group of White Leghorns and of Rhode Island Reds, respectively   For the White Leghorns, second-year production was about 28 per cent less than first-year production, and third-year production was about 13 per cent less than second-year production   For the Rhode Island Reds, second-year production was about 31 per cent

Fio 87 Showing the decline in annual egg production in White Leghorns and Rhode Island Reds, respectively   (Chart made from data of Insko, Steele, and Wightman, 1947)

less than first-year production, and third-year production was about 24 per cent less than second-year production

Interesting data on the decline in yearly egg production over a period of 10 years in a flock of 200 White Leghorns in which no culling was practiced have been made available by Clark (1940)   The egg-production records given in Table 18 pertain to survivors at the end of each laying year

The data in Table 18 indicate that, over a period of years in large unculled flocks, the percentage of decline in yearly egg production would be at a fairly regular rate in the absence of mortality from an epidemic any given year

Among 243 Rhode Island Reds, Hays (1913) observed that their first-year average of 257 eggs dropped to a second year average of 171 a decline of about 31 per cent   In 1919, Hays reported a first-year average of 252 eggs and a second-year average of 152 eggs among 118

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Sustained High Yearly Production. Although it has been shown that egg production normally declines each successive year, there are instances in which a high level of egg production has been sustained over a period of years From the standpoint of the poultry breeder, birds that lay well over a period of years may prove to be valuable breeders, especially if by progeny testing they have demonstrated their ability to transmit high laying ability. Such birds have demonstrated that they had the ability to resist the organisms of disease that are usually present on most poultry plants A number of private breeders and a few experiment stations have reported records of egg production of over 1300 eggs In Table 20 are given the records of some experiment-station birds, together with the approximate age of the bird at the time the record was made, the data having been supplied by Martin (1940)

TABLE 20

LONGEVITY RECORDS OF EGG PRODUCTION

(Martin 1940)

Station	Breed	Age	Number of Eggs
Cornell University	White Leghorn	8	1715
Iowa Exp Station	White Leghorn	7	1704
Ky Exp Station	White Leghorn	7	1187
Ky Exp Station	White Leghorn	8	1475
Iowa Exp Station	White Leghorn	9	1472
Purdue Exp Station	White Leghorn	10	1421
Ore Exp Station	Oregon	9	1335
Wis Exp Station	White Leghorn	9	1335
Utah Exp Station	White Leghorn	9	1325
Mo Exp Station	White Leghorn	10	1310

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Wis Exp Station	White Leghorn	9	1335
Utah Exp Station	White Leghorn	9	1327
Mo Exp Station	White Leghorn	10	1310

Moreover, in crosses involving the sex-linked genes for silver and barring, Punnett (1930) secured results that led him to conclude that egg production is not sex-linked in its inheritance. Punnett mated an Indian Game male from a strain showing low fecundity to a White Wyandotte female that laid 240 eggs in her first laying year and came from a strain showing high fecundity. The F_1 males were all silver-barred, indicating that the White Wyandotte female carried both silver and barring.

An F_1 male was mated to Silkie females showing low fecundity. The results secured indicate the absence of sex linkage in the inheritance of egg production. The mean egg production per bird of the 21 barred females was 123.7 eggs, for the 18 nonbarred females, it was 118.1 eggs, for the 28 silver females, it was 113.0 eggs, for the 11 gold females, it was 142.1 eggs. The number of birds in each of the four groups is rather small, but the results, taken together with other results secured by Punnett, do not seem to support the theory of the inheritance of egg production on a sex-linked basis.

A Light Sussex female that laid 200 eggs in her first year of laying was mated with the same Indian Game male that Punnett mated with the White Wyandotte female mentioned previously. The Light Sussex carries the sex-linked gene for silver, the female, of course, being hemizygous. The F_1 males carry silver, and one of them was mated to Silkie females. The results obtained show that the gold females laid somewhat better than the silver females, exactly opposite to expectation on the assumption of sex linkage for egg production.

The breeding of Rhode Island Reds for high egg production at the Massachusetts Agricultural Experiment Station over a period of years enabled Goodale and MacMullen (1919) and Goodale and Sanborn (1922) to develop the conception that the first-year egg production of a bird is determined by the following five different factors:

1. Age in days that laying commences or sexual maturity
2. Rate of laying or intensity of production
3. The amount of broodiness
4. Pauses in production, especially winter pause
5. Persistency of production

The results of further breeding work with the same flock of Rhode Island Reds was reported upon by Hays and Bennett (1923) and Hays and Sanborn (1927b).

These early reports stimulated interest among others, particularly with respect to investigations concerning the relative influence of the five factors in determining egg production.

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Byerly and Knox (1946) compared the average age at commencement
of laying among groups of Rhode Island Red and White Leghorn pullets
hatched mostly between March 17 and May 12 during the years 1936–
1945. During each year through 1944, artificial light was provided

Fig 89. Age at first egg in relation to date of hatch The upper solid line and dots
and the lower solid line and circles pertain to the 1937–1941 and the 1945 Rhode
Island Red pullets, respectively. The upper dash line and dots and the lower dash
line and circles pertain to the 1936–1944 and 1945 White Leghorn pullets, respectively
(Byerly and Knox, 1946)

from 5 A.M. to 8 A.M. from October 15 to about May 1; in 1945 artificial
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1937–1941 Rhode Island Red pullets that were hatched during the week
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For the most part, in a given strain of birds, those which commence laying the latest are the largest at that time, as Lerner (1946) has shown. By selecting White Leghorns for breeding purposes for longer shanks, both age at first egg and body weight at that time were increased. On the other hand, Hays and Sanborn (1939), over a period of several years, maintained age at first egg in Rhode Island Reds at a relatively constant level while at the same time increasing body size at first egg, thus demonstrating that age at sexual maturity is inherited independently of body size.

Inheritance of Sexual Maturity   There seems little doubt that age at sexual maturity is inherited.   Goodale and Sanborn (1922), with Rhode Island Reds, succeeded in reducing age at sexual maturity from 256 days in 1913 to 194 days in 1918.   Hays (1924) was the first to suggest that sex-linked, as well as autosomal, genes are involved in the inheritance of age at first egg.   The sex-linked inheritance of age at sexual maturity was confirmed by Warren (1930, 1934) in crosses between White Leghorns and Rhode Island Reds.   On the other hand, results secured by Hazel and Lamoreux (1947) and Lerner and Cruden (1951) failed to indicate sex-linked inheritance of sexual maturity.

Inbreeding in Rhode Island Reds was found by Hays (1934) to retard sexual maturity, although Waters and Lambert (1936) observed that rather intensive inbreeding in a late-maturing strain of White Leghorns did not retard sexual maturity.   Maw (1942) reported that the inbred strains with which he worked had a mean age at first egg of 216 days as compared with 195 days for nonimbreds, a difference of 21 days. Among fifteen inbred lines of White Leghorns, Waters (1945) secured results which indicated that among eleven of the lines inbreeding caused practically no change in age at sexual maturity whereas in the other four lines age at sexual maturity increased during the last two generations reported upon.

Heritability of Sexual Maturity   The relatively low levels of heritability (see Chapter 12) of age at sexual maturity reported by Lerner and Taylor (1943), Lerner (1945), Hazel and Lamoreux (1947), Shoffner and Sloan (1948), and Lerner and Cruden (1951) indicate that progeny testing would be necessary to improve this character maternally in any strain.

In selecting future breeding stock on a family basis, Lerner and Taylor (1940c) suggested that determining the rating of various families on the basis of the *median* rather than the *mean* age at first egg was the more expedient of the two methods, the median being the midpoint in the frequency distribution of the full sisters with respect to age at first egg.   The advantage of the median over the mean lies in the fact that

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Broodiness. There are breed differences with respect to the amount of broodiness among laying flocks White Leghorns usually exhibit much less broodiness than most general-purpose breeds whereas Cornish usually exhibit much more broodiness than general-purpose breeds Also, within a given breed or variety there are strain differences in the amount of broodiness exhibited by the laying stock, depending upon the extent to which selection and breeding have been carried on to reduce broodiness It is quite obvious, therefore, that broodiness is inherited, as Goodale, Sanborn, and White (1920) originally suggested

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	1923	1924	1925	1926	1927	1928	1929	1930	1931
Nonbroody line	222	186	201	210	215	208	192	224	222
Broody line	174	163	183	165	188	182	184	181	180
Difference	48	23	18	45	27	26	8	43	42

When all birds were considered, the nonbroody line averaged 210 eggs as compared with the broody line average egg production of 179 eggs, a difference of 31 eggs per bird

Knox, Jull, and Quinn (1935), in a flock of Rhode Island Reds in which broodiness was not considered in the selection and breeding program, observed that broody birds started to lay later in life, laid at a relatively slower rate, and were less persistent in production than nonbroody birds On the other hand, Hays (1944a), in the same strain of Rhode Island Reds reported upon previously but in which broodiness was considered in the selection and breeding program, reported an average egg production of 269 eggs for broody birds as compared with an average of 272 eggs for nonbroody birds Likewise, Lamson (1948), in another strain of Rhode Island Reds reported an average egg pro-

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Burrows and Byerly (1936) and Byerly and Burrows (1936) concluded that the anterior pituitary in broody hens secretes more prolactin than the anterior pituitary of layers in continuous production (see Chapter 2 for a discussion of hormone secretions in the fowl) Byerly and Burrows also showed that the anterior pituitary of males secretes about the same amount of prolactin as the anterior pituitary of genetically nonbroody females

Nalbandov and Card (1945) demonstrated that Cornish, White Leghorn, and White Plymouth Rock males were induced to brood chicks but not incubate eggs by appropriate injection of prolactin Nalbandov, Hochhauser, and Dugas (1945) concluded that prolactin inhibits the production of the follicle-stimulating gonadotropic hormone of the anterior pituitary Normal, sexually mature males injected with prolactin had testes that were considerably reduced in size, this having been brought about by the shutting off of the gonad-stimulating hormone

The possibility of interrupting broodiness by injecting synthetic drugs having the effects of female sex hormones was demonstrated by Godfrey and Jaap (1950) When 15 mg of diethylstilbestrol in 1 ml of sesame oil was injected subcutaneously into broody birds on the site of the apteria (the area between the feather tracts) along the breast, broodiness was terminated in over 75 per cent of the broody birds that were treated The injection of 30 mg of diethylstilbestrol in 2 ml of sesame oil proved to be almost completely effective in general-purpose breeds However, three injections of 30 mg of diethylstilbestrol over a 12 day period failed to terminate broodiness in a Dark Cornish female

Genetics of Broodiness Punnett and Bailey (1920) concluded that broodiness is apparently due to more than one independent autosomal gene Warren (1930) made reciprocal matings between White Leghorns and Rhode Island Reds and observed a considerable difference in the amount of broodiness between the daughters of the two matings Roberts and Card (1933) made reciprocal matings between White Leghorns and Dark Cornish and reported that 37 per cent of the daughters of the White Leghorn sire × Dark Cornish dams were broody an average of 2 1 times whereas 88 per cent of the daughters of the Dark Cornish sire × White Leghorn dams were broody an average of 3 7 times These results indicate that at least one sex-linked gene is involved in the inheritance of broodiness The results secured by Kaufman (1948) from reciprocal matings between White Leghorns and Polish Greenlegs led her to conclude that a sex-linked gene and at least one autosomal gene are involved in broodiness

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Persistency of Production. From a biological standpoint, the first laying year includes the period from commencement of laying to the cessation of egg production preceding the onset of the first complete molt. In almost any flock there are a few exceptions to cessation of egg production preceding the first complete molt, since it is well known that a few of the best layers continue laying while molting. It is obvious, of course, that the earlier that molting begins in relation to commencement of laying, the shorter the period of production. For most poultry breeders the first laying year is 365 days from commencement of laying, the onset of molting occurring in a portion of the flock before the termination of the first laying year.

Marble (1930) showed that, among the poorest layers in a flock, little if any molting occurred before complete cessation of laying whereas, among the best layers in a flock, molting sometimes began before cessation of laying. Hays and Sanborn (1930), using the 365-day laying year, showed that the longer the duration of the molting period, the lower the first-year egg production tended to be for Rhode Island Reds Hendricks (1933) observed that, among White Leghorns which had begun their first-year molt relatively early, the duration of molt was longer than among late molters Knox, Jull, and Quinn (1935) considered the number of eggs laid in August and September at the end of the first laying year as a criterion of relative persistency. Hays (1936b) suggested that the dividing point between high persistency and low persistency phenotypes was about 270 days from commencement of laying in Rhode Island Reds hatched at approximately the same time Lerner and Taylor (1937b) observed that date of last egg served as a slightly better index of persistency than age at last egg in their White Leghorns but suggested that age could be used if corrected for hatching date.

It was once believed by some investigators that age at last egg or date of last egg prior to the first complete molt was the most important factor determining first-year egg production. It is now realized, however, that in order to turn in a superior first-year record a bird must commence laying relatively early in life, lay at a good rate, and persist in production for approximately 10 months. Very probably the genes determining the total number of eggs laid during the first laying year are the same genes, for the most part, that determine age at sexual maturity, rate of laying, and persistency of production. This conclusion would seem to be borne out by the previously reported observation of Lerner and Cruden (1948) that in their White Leghorns the heritability of accumulative egg production was nearly constant throughout the year.

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laying year. The inherent difficulty in attempting to appraise the five factors with respect to their relative importance is due to the rather arbitrary basis on which some of the factors were established.

INBREEDING AND CROSSBREEDING

Programs of inbreeding for the purpose of developing superior laying strains are the outgrowth chiefly of the results secured in the production of hybrid corn through inbreeding. Another factor is the difficulty that numerous poultry breeders have experienced in still further increasing the level of egg production over that attained by the progeny-testing methods of selection and breeding carried on for several years without inbreeding.

The results secured from the early investigations on inbreeding for increased egg production (Dunn 1923, Hays 1929, 1934, Dunkerly 1930, and Jull 1933) were consistent in showing that inbreeding lowered egg production. The results of other inbreeding experiments, reported in previous chapters, have shown that hatchability of eggs and viability of chicks were affected so seriously that in numerous cases entire families were lost. The net result of the early work on inbreeding was to demonstrate the importance of starting with carefully selected strains of superior breeding quality.

The first purpose of inbreeding is to develop strains of birds relatively homozygous for genes determining high egg production. Close inbreeding frequently reveals the presence of undesirable genes in the parental stock. That is why rigid selection of the inbred progeny each succeeding generation is imperative in order that variability may be reduced.

The second purpose of inbreeding is to develop inbred lines of a breed or variety for the purpose of crossing them with inbred lines of another breed or variety (see discussion of crossbreeding, which follows). An inbred line is recognized as such when its progeny has a coefficient of inbreeding in excess of 50 per cent (see Chapter 12 for a discussion of coefficients of inbreeding). Full-brother × full-sister matings for 3 successive years produce progeny that is 50 per cent inbred. Therefore, some additional inbreeding is necessary for the progeny to be able to qualify as an inbred line.

Warren (1950) stated that in developing inbred lines it seems desirable to accelerate the inbreeding program by developing a large number of inbred lines at the start, eliminating many of the lines after one generation of inbreeding, and then repeating this procedure for 2 or 3 years with a view toward securing a reasonable number of promising

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progenies produced by crossing different inbred lines of White Leghorns

The data of Knox (1950), given in Table 22 are first-year egg production records for 1946–1947 and 1947–1948, respectively, of the progenies secured from outbreeding, crossbreeding and crossing inbred lines (hybridization) An outbreak of Newcastle disease during the 1947–1948 laying year resulted in lowering egg production somewhat as compared with the 1946–1947 laying year

In Table 22 it is shown that the progeny of the mating (2) of outbred

TABLE 22

Average First Year Egg Production of Progeny in Relation to Kinds of Matings

(Knox 1950)

Mating	Kind of Mating	Average First-Year Egg Production of Progeny	
		1946–1947	1947 1948
1	Outbred R I Red ♂♂ × outbred R I Red ♀♀	219	199
2	Outbred R I Red ♂♂ × outbred W Leghorn ♀♀	229	208
3	Inbred R I Red ♂♂ × inbred W Leghorn ♀♀	239	230
4	Outbred W Leghorn ♂♂ × outbred R I Red ♀♀	250	240
5	Inbred W Leghorn ♂♂ × inbred R I Red ♀♀	255	240
6	Outbred W Leghorn ♂♂ × outbred W Leghorn ♀♀	221	182

Rhode Island Red males and outbred White Leghorn females laid slightly better both years than the outbred Rhode Island Red (1) and outbred White Leghorn progenies (6) In other words, crossbreeding was beneficial

In Table 22 it is also shown that the progeny of the mating (3) of inbred Rhode Island Red males and inbred White Leghorn females laid better both years than the progeny of the mating (2) of outbred Rhode Island Red males and outbred White Leghorn females On the other hand, the progeny of outbred White Leghorn males and outbred Rhode Island Red females (4) laid better both years than the progenies of any of the previously mentioned matings Finally, the progeny of the mating of inbred White Leghorn males and inbred Rhode Island Red females (5) laid practically the same number of eggs as the progeny of the mating (4) of outbred White Leghorn males and outbred Rhode Island Red females Crossing inbred lines of two different breeds yields hybrid progeny, according to modern terminology

The progeny of White Leghorns crossed with general purpose breeds or varieties lay tinted eggs, a factor of some importance to those selling eggs on a market that offers a preference for eggs with white shells

progenies produced by crossing different inbred lines of White Leghorns

The data of Knox (1950), given in Table 22 are first-year egg production records for 1946–1947 and 1947–1948, respectively, of the progenies secured from outbreeding, crossbreeding and crossing inbred lines (hybridization) An outbreak of Newcastle disease during the 1947–1948 laying year resulted in lowering egg production somewhat as compared with the 1946–1947 laying year

In Table 22 it is shown that the progeny of the mating (2) of outbred

TABLE 22

Average First Year Egg Production of Progeny in Relation to Kinds of Matings

(Knox 1950)

Mating	Kind of Mating	Average First-Year Egg Production of Progeny	
		1946–1947	1947 1948
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other strains of Light Sussex and Rhode Island Reds quite different results might be secured

Data presented by Brunson and Godfrey (1951) indicate that crossbreeding does not always result in increased egg production For instance, the three-way cross pullet progeny secured from mating White Leghorn males to the F_1 black pullets from matings of Rhode Island Red ♂♂ × Barred Plymouth Rock ♀♀ did not lay as well as White Leghorn pullets of the parental strain nor as well as F_1 black pullets The F_1 black pullets, however, laid better than pullets of the Rhode Island Red and Barred Plymouth Rock parental strains

Among strain and breed crosses involving eight strains representing Australorps, Barred Plymouth Rocks, New Hampshires, and Rhode Island Reds, Ghostley and Nordskog (1951) secured about 9 per cent better egg production from the crossbred and strain-cross progenies than from the purebred progenies, some of this increase in egg production being due to earlier sexual maturity of the crossbred and strain-cross progenies Hutt and Cole (1951) secured better egg production from the progeny secured from crossing two strains of White Leghorns than from the progeny of each strain, some of the increase in egg production being due to earlier sexual maturity of the strain-cross progeny King (1951) crossed different parental strains of Barred Plymouth Rocks and Rhode Island Reds reciprocally and compared the egg production of their progenies with purebred progenies The progeny secured from matings of Barred Plymouth Rock males and Rhode Island Red females laid an average of 21 more eggs per year during four years than the highest of the other matings It was suggested that this increase in egg production may have been due to sex-linkage

SUMMARY—DEVELOPING OUTSTANDING LAYING STRAINS

The previous discussion in this chapter has dealt with the major problems involved in the transmission of laying ability and problems related thereto Numerous poultry breeders have found that, by following certain procedures in the selection of breeding stock each year, it is possible to develop strains averaging well over 200 eggs on a henhoused basis and over 240 eggs for birds that complete the first laying year These same breeders have naturally found, however, that, as the level of egg production is increased, further progress becomes increasingly difficult Therefore, they seek further refinements in breeding procedures and selection methods with a view toward developing outstanding laying strains

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suggested that the average complete first year egg production of six full sister daughters serves as a reliable index of the dam's ability to transmit high egg production Females for future breeding purposes should be selected first from among the progeny of each sire that proved to be superior in transmitting high egg production and second from among the full-sister progeny of each superior dam

The ability to identify sires of outstanding breeding worth is relatively more important than the ability to identify dams of outstanding breeding worth This is because each sire has several times as many daughters as has each dam to which he is mated Apparently, the average complete first-year egg production of from 30 to 40 daughters of a sire serves a reliable index of the sire's ability to transmit high egg production Males for future breeding purposes should be selected on the same basis as females

Increasing the Number of Males Progeny Tested Since it is important to be able to identify as many superior males as possible changing males in the middle of the breeding season is recommended This makes possible the testing of twice as many males The first male in the breeding pen is removed 5 days before the second male is placed in the pen During these 5 days all chicks secured from the pen may be credited to the first sire Beginning 5 days after the second male is placed in the pen, all chicks secured from the pen may be credited to the second male Thus only 5 days are lost, when the male parentage of chicks secured is questionable If the females in the pen are artificially inseminated with the semen of the second male on the sixth and seventh days after the first male was removed from the pen all chicks secured from the pen beginning with the eighth day after the removal of the first male can be credited to the second male Thus only 2 days are lost

Progeny Testing Pullet Breeders The progeny-test method of identifying superior sires and dams and of selecting future breeding stock from the superior families, as indicated by the first year laying performance of families of full sisters (dam's progeny) and families of half sisters (sire's progeny), means a delay of one generation in breeding procedure Of course, sires and dams that have been proved by progeny testing to be superior in transmitting high egg production should be used the next year and perhaps longer Their daughters however are about 18 months old before the superior families are identified as such

Many poultry breeders would probably make more progress in developing outstanding laying strains by selecting pullet breeders in December of the year in which they were hatched or in the following January The pullets would be less than 1 year old Lerner and Cruden (1948) observed that "the amount of genetic gain per generation when

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3 In carrying on a breeding program to develop a high laying strain, what are the more important environmental factors affecting egg production that should be kept as uniform as possible from year to year?

4 Discuss the problem of culling pullets from the standpoint of having a sufficient number of birds per family at the end of the laying year and also from the standpoint of securing a reasonably reliable index of first-year egg production per family

5 To what extent may mortality during the first laying year give a wrong impression of the breeding worth of a sire and dam as judged by the average egg production of the survivors among their progeny?

6 Tell what programs of trapnesting can be carried on to enable the poultry breeder to arrive at a reliable estimate of first-year egg production per bird and per family of full sisters and half-sisters

7 What is the relationship between annual egg production and age of layers?

8 What is the relative importance of the five different factors determining first-year egg production?

9 (a) How may date of hatch affect sexual maturity?

(b) Approximately what body weight should Leghorn and general purpose pullets attain at commencement of laying?

(c) What is the advantage of determining the *median* age at first egg rather than the *mean* age at first egg?

(d) Discuss the relative significance of broodiness in relation to maintaining high egg production from year to year

10 (a) Discuss the principal features involved in producing hybrid pullets

(b) Outline the essential features of a sound progeny testing program designed to develop a superior laying strain

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II · Egg Characters

Several egg characters are of economic importance to egg producers, distributors, and consumers These various characters determine egg quality, which is the condition of shell and contents of eggs which affects consumer appeal Since the characters determining quality have a hereditary basis, poultry breeders are concerned in doing whatever is possible to produce eggs of superior quality

EGG SIZE

The standard market size in eggs is 24 ounces per dozen or 2 ounces per egg, which is equivalent to 56 7 grams Egg cases, with their flats and fillers, are constructed to accommodate eggs of standard size, each egg fitting into its compartment in such a manner that breakage is kept at a minimum when eggs are shipped to market When extra large

JUMBO	EXTRA LARGE	LARGE	MEDIUM	SMALL	PEEWEE
30 oz.	27 oz.	24 oz.	21 oz.	18 oz.	15 oz.

Fig 91   Egg weight according to size class   (U S Dept Agr)

eggs or those with thin shells are packed in cases, excessive breakage often results

Practically all flocks produce eggs showing considerable variation in size, perhaps as much as represented in Fig 91, which gives the size for each of six different grades of eggs

Egg size and egg weight are synonymous terms so far as newly laid eggs are concerned The larger the size, the heavier the egg On the other hand, among stale eggs a large egg may be much lighter in weight than a smaller one because of the loss through the porous shell of much

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causes them to lay smaller eggs, according to Buckner (1927) A deficiency of vitamin D results in decreased egg weight, according to Parkhurst (1933) These are but a few of the illustrations that might be cited to show how the kind of diet fed to layers may adversely affect egg weight

Jeffrey (1941a) pointed out that the approximate date that pullets are hatched may affect their first-year mean egg weight He showed that pullets hatched in November and January produced more small and very small eggs than pullets hatched in April June and September One of the contributing factors tending to reduce egg size according to the hatching date of the pullets was the atmospheric temperature prevailing during the period when the pullets commenced laying and for a period thereafter

The fact that high summer temperatures tend to reduce the size of eggs laid has been pointed out by Bennion and Warren (1933a) Warren (1939), and Yeates, Lee, and Hines (1941) It has been pointed out by Warren (1948) and Warren, Conrad Schumacher and Avery (1950), however, that in the more northern latitudes the size of egg laid increases rather steadily throughout the first laying year if summer temperatures are not sufficiently high to bring about a decrease in size Hays (1948) reported that, over a 6-year period summer temperatures as high as 85° F failed to reduce egg size perceptibly in Rhode Island Reds

Wilson (1948) demonstrated that the body temperature of White Leghorns rose sharply as the environmental temperature was increased from 90° F to 105° F and feed consumption decreased noticeably when the environmental temperature was above 100° F Wilson (1949) found that, when the environmental temperature was 100° F, feed consumption was only 42 per cent as much as when the environmental temperature was 70° F It seems logical to suggest, therefore, that when hot summer weather is of sufficient duration, feed consumption is decreased sufficiently to bring about a decrease in body weight and a decrease in egg size

Egg Weight by Breeds and Varieties Although the consensus is that, within a given flock, large birds tend to lay larger eggs than small birds, it does not follow that Jersey Black Giant pullets lay eggs twice as large as those laid by White Leghorn pullets although the standard body weights are 8 pounds and 4 pounds, respectively Funk and Kempster (1934) and Hall (1939) have shown that differences in mean annual egg weight among strains of the same breed or variety are sometimes greater than differences in mean annual egg weight among different breeds and varieties

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monthly mean egg weight in both groups was attained in February
The mean annual egg weight for the birds that commenced laying in
December was greater than the mean annual egg weight for the birds
that commenced laying in September   Henderson (1938) showed that
from October through February there was a progressive monthly in-
crease in egg weight and body weight for eight pens of White Leghorns

The increase in mean egg weight per month from October through
February and March, respectively, for Rhode Island Reds in 1930 and

Fig 93   Mean monthly egg weight in grams per egg and ounces per dozen for Rhode
Island Red pullets in 1930 and 1943 respectively   (Hays 1944)

1943 is shown graphically in Fig 93 (Hays 1944)   In both years, mean
monthly egg weight increased at about the same rate but continued for
one month longer in 1943 than in 1930   Note particularly the effects
of selection for increased egg size during a period of 13 years as evidenced
by the 1943 mean monthly egg weights as compared with the 1930 mean
monthly egg weights   Also note that after mean monthly egg weight
reached its maximum in February and March, respectively, there was a
progressive decrease in mean monthly egg weight for 2 months

Maw and Maw (1932), from observations on egg weights in a flock
of White Leghorns, concluded that those birds whose first ten eggs aver
age less than 47 5 grams, about 1 67 ounces are not apt to lay eggs
throughout the year that average 21 ounces per dozen   In White Leg
horns, Rhode Island Reds and Barred Plymouth Rocks Wilson and
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laying commenced   October or earlier, 16 grams or 19 4 ounces per

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least the following specified weights depending upon the month when
laying commenced   October or earlier, 46 grams or 19 4 ounces per

The data in Table 25 show that the White Plymouth Rocks which commenced laying at 225 days or earlier laid relatively smaller eggs, both for the first 10 eggs and for the year's production, than later-maturing birds Also, the maximum monthly egg weight of the group of earlier-maturing birds was lower than that of the later-maturing birds

The possibility of developing strains of pullets that will lay eggs of standard or maximum monthly weight as early as December, is shown in Table 26

Olsen and Knox secured the results given in Table 26 by selecting breeding stock each year on the basis of the relative earliness that eggs attained standard egg weight or better

Egg Weight and Body Weight at Sexual Maturity. Hays (1933), in Rhode Island Reds, and Funk (1935), in White Plymouth Rocks, observed significant positive correlations between egg weight and body weight at commencement of laying In Barred Plymouth Rocks and White Leghorns, Callenbach (1934) observed a significant positive correlation between weight of first egg and body weight at commencement of laying These three observations mean that the later in life that laying commences the larger is the body size and the larger is the egg produced at that time

The relationship between the weight of eggs for different periods and body weight at sexual maturity in White Plymouth Rocks is given in Table 27

TABLE 27

AVERAGE WEIGHT OF EGGS, IN GRAMS PER EGG AND OUNCES PER DOZEN, FOR DIFFERENT PERIODS IN RELATION TO BODY WEIGHT, IN POUNDS, AT SEXUAL MATURITY, IN WHITE PLYMOUTH ROCKS

(Funk and Kempster 1934)

Body Weight at Sexual Maturity in Pounds	Average Weight First Ten Eggs		Average Egg Weight for Year		Maximum Monthly Egg Weight	
	Grams per egg	Ounces per dozen	Grams per egg	Ounces per dozen	Grams per egg	Ounces per dozen
3 6-4 5	47 8	20 3	54 9	23 3	56 8	24 0
4 6-5 5	52 4	22 2	55 2	23 4	57 5	24 4
5 6-6 5	54 8	23 2	56 6	24 0	58 4	24 7
6 6-7 5	58 3	24 7	59 9	25 3	61 2	25 9

The data in Table 27 show that the smaller the size of the bird at commencement of laying, the smaller were the eggs laid at that time and throughout the year In addition, the maximum monthly egg

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The data in Table 27 show that the smaller the size of the bird at commencement of laying, the smaller were the eggs laid at that time and throughout the year   In addition, the maximum monthly egg

Hays stated that the eggs of pullets laying very large clutches during the first laying year are less variable in weight than eggs of pullets laying small clutches

These findings are in conformity with the observations of Atwood (1927) and Funk and Kempster (1934) to the effect that eggs laid during the early morning hours are usually larger than those laid about noon or after, since many of the early morning eggs are first eggs in a clutch

Selecting Breeding Stock on Basis of Egg Weight. The practice of weighing all eggs laid by each bird during the first laying year, carried on by some poultry breeders several years ago, involves much labor   That this is unnecessary was shown by Jull (1930), Dudley (1931), Maw and Maw (1932), A B Godfrey (1933), Hays (1937), Jeffrey (1938), and Schnetzler (1946), all of whom showed that a reliable estimate of the mean first-year egg weight could be obtained by weighing eggs at periodic intervals or for a few days in succession for short intervals of time

The qualifying average egg weight for pullets entered in the ROP phase of the National Poultry Improvement Plan is 24 ounces   At least 8 eggs are weighed, weighings being made either during 4 consecutive days each month or on the same day each week for any 4 consecutive months between January 1 and July 1   Poultry breeders trapnesting their pullets 3 days a week weigh the eggs on 3 consecutive days each month for 5 consecutive months or on the same day each week for any 4 consecutive months between January 1 and July 1

Breeding for Good Egg Weight. Inbreeding apparently has little effect on egg weight, according to the observations of Waters and Lambert (1936), Waters (1945b), Shoffner (1948), and Hays and Talmadge (1949)   Shoffner also observed that inbreeding had little effect on body size

Ghigi (1948) made reciprocal matings between representatives of *Gallus sonnerati* and White Leghorns and secured results indicating sex linkage in the inheritance of egg weight   The average weight of the *Gallus sonnerati* eggs was 30 grams and that of the White Leghorn eggs 55 grams   The progeny secured from the mating of White Leghorn ♂ × *Gallus sonnerati* ♀ laid eggs averaging 56 7 grams, whereas the progeny secured from the mating of *Gallus sonnerati* ♂ × White Leghorn ♀ laid eggs averaging 32 6 grams   Waters and Weldin (1929) and Hays (1941), reported, however, a lack of sex linkage in the inheritance of egg weight   Olsen and Knox (1940) concluded that sire and dam contribute equally to the inheritance of egg weight   Waters (1941, 1945a), from investigations with inbred White Leghorns, was led to

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These findings are in conformity with the observations of Atwood (1927) and Funk and Kempster (1934) to the effect that eggs laid during the early morning hours are usually larger than those laid about noon or after, since many of the early morning eggs are first eggs in a clutch

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The qualifying average egg weight for pullets entered in the ROP phase of the National Poultry Improvement Plan is 24 ounces At least 8 eggs are weighed, weighings being made either during 4 consecutive days each month or on the same day each week for any 4 consecutive months between January 1 and July 1 Poultry breeders trapnesting their pullets 3 days a week weigh the eggs on 3 consecutive days each month for 5 consecutive months or on the same day each week for any 4 consecutive months between January 1 and July 1

Breeding for Good Egg Weight. Inbreeding apparently has little effect on egg weight, according to the observations of Waters and Lambert (1936), Waters (1945b), Shoffner (1948), and Hays and Talmadge (1949) Shoffner also observed that inbreeding had little effect on body size

Ghigi (1948) made reciprocal matings between representatives of *Gallus sonnerati* and White Leghorns and secured results indicating sex linkage in the inheritance of egg weight The average weight of the *Gallus sonnerati* eggs was 30 grams and that of the White Leghorn eggs 55 grams The progeny secured from the mating of White Leghorn ♂ × *Gallus sonnerati* ♀ laid eggs averaging 56 7 grams, whereas the progeny secured from the mating of *Gallus sonnerati* ♂ × White Leghorn ♀ laid eggs averaging 32 6 grams Waters and Weldin (1929) and Hays (1941), reported, however, a lack of sex linkage in the inheritance of egg weight Olsen and Knox (1940) concluded that sire and dam contribute equally to the inheritance of egg weight Waters (1941, 1945a), from investigations with inbred White Leghorns, was led to

From the data given in Table 28, it is to be noted that the increase in total weight of eggs produced per bird from 1923 through 1946 amounted to over 75 per cent, a remarkable achievement

EGG SHAPE

The production of eggs of good shape is important from the marketing standpoint   Standard egg cases, flats, and fillers accommodate eggs not over 2 13/32 inches long and 1 25/32 inches wide, a ratio of 1 to 0 74   Excessively long eggs are liable to be crushed, and excessively wide ones are difficult to fit into the fillers properly

From studies on the relationship between egg weight and egg shape by Pearl (1909), Curtis (1914), Pearl and Curtis (1914), and more particularly Pearl and Surface (1914), it has been shown that egg weight is more highly correlated with egg breadth than with egg length   This observation has been confirmed by Asmundson (1931), who also found that albumen weight and shell weight are each more highly correlated with egg breadth than with egg length

For the most part, all eggs laid by each bird are of a characteristic shape   In other words, egg shape is a hereditary character   The problem of the variation in the shape of eggs was investigated extensively by Asmundson (1931), who concluded that there are three factors that determine the general shape of an egg   first, the amount of albumen secreted in the albumen-secreting portion of the oviduct, second, the size of the lumen of the isthmus and the albumen-secreting portion of the oviduct, third, the muscular activity of the walls of the isthmus and the albumen-secreting portion of the oviduct   It was further concluded that the general shape may be more or less altered in the uterus, which, together with the isthmus, gives each egg its particular shape   According to Asmundson and Jervis (1933), the shape of the egg is determined for the most part while it is in the isthmus, the uterus exercising little effect, although Asmundson and Burmester (1938) observed that resecting part of the uterus induced changes in egg shape   Harper and Marble (1945a, 1945b) concluded that the albumen secreted by the oviduct does not influence egg shape and that the shape of the egg is determined by the time it has passed through the narrowest section of the oviduct

Egg shape is measured by determining shape index   The greatest width is divided by the greatest length, and the product is multiplied by 100   Baten and Henderson (1941) observed that in their strain of Barred Plymouth Rocks the egg-shape index was 71 9 and in their

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Obviously several genes are involved. Hall (1944) crossed White Leghorns and Rhode Island Reds and secured similar results, although there was some evidence of sex linkage. Blow, Bostian, and Glazener (1950) studied the inheritance of intensity of shell pigmentation in Barred Plymouth Rocks and Rhode Island Reds and found no evidence of sex linkage. Genes for darkest-colored shells exhibited dominance over genes for lightest-colored shells. From the standpoint of reliability in candling market eggs, poultry breeders apparently should be interested in developing strains of birds that lay light brown eggs of uniform shade. Poultry breeders who develop inbred lines for crossing to produce hybrid pullets should keep in mind that tinted eggs are laid by the progeny of crosses between "white-egg" breeds and "brown-egg" breeds. This is a matter of some concern to producers who cater to a market showing a preference for white eggs.

Leghorns that lay tinted eggs for a considerable period of time should not be used for breeding purposes, nor should their brothers be used. The blue shell color of the Araucana proved to be dominant to white shell in tests conducted by Punnett (1933).

For many years, there was a belief among a few poultry fanciers that the phenomenon known as "xenia" really occurred. This belief was based upon the supposition that the semen of a Rhode Island Red or other "brown-egg" male mated to a White Leghorn or other "white-egg" female would cause her to lay brownish-tinted eggs. Also, if a "white-egg" male were mated to a "brown-egg" female, she would lay light brown eggs. Kopec (1926) and Axelsson (1932) disproved the belief.

SHELL QUALITY

Shell quality characteristics include the finish, texture, and thickness of shells.

The enormous breakage of eggs that occurs every year on farms and in marketing channels is due to a considerable extent to shells of poor quality. Thinness of shell is apparently the most important factor responsible for the breakage that occurs, especially in marketing channels. Thick shells are necessary to enable eggs packed in cartons and cases to withstand the shock that often results from rough or careless handling.

Breaking Strength and Shell Thickness. Various devices have been used by different investigators for determining the breaking strength of the shells of chicken eggs. According to Kimball (1950) these devices may be classified, according to the nature of the force employed to break the shell, into (1) crushing, (2) penetrating, and (3)

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Unless the diet of hens contains a sufficient amount of calcium, egg shell thickness is reduced. Bennion and Warren (1933a) were among the first to point out that high atmospheric temperatures induce layers to produce thin-shelled eggs. Miller and Bearse (1934) observed that the percentage of shell in eggs began to decrease in March and continued to decrease until October. Conrad (1939) showed that, when atmospheric temperature increased from 70° F. to 90° F., the blood calcium level was decreased by 25 to 30 per cent. Warren and Schnepel (1940) reported that, when birds were subjected to a temperature of 90° F., the calcium content of the blood was reduced to about the same extent as was shell thickness. Wilson (1949) found, not only that shell thickness decreased when the air temperature rose much above 70° F., but also that feeding thyroprotein (iodinated casein), a substance having the properties of thyroxine, increased shell thickness.

The thickness of shells of eggs in relation to their position in the clutch was investigated by Wilhelm (1940) and Berg (1945). Wilhelm reported relatively little decrease in shell thickness between the first and last eggs of the same clutch in two-, three-, or four-egg clutches. Berg, however, observed that the shell of the second egg of two-egg clutches was thicker than that of the first egg of the clutch. In three-egg clutches and those of greater egg numbers, the first and last egg of the clutch had thicker shells than those of intervening eggs.

The poultry breeder must keep in mind that an outbreak of disease in the flock may affect shell thickness adversely. Scott, Jungherr, and Matterson (1944) pointed out that sulfanilamide (sometimes used in outbreaks of infectious coryza) tends to reduce shell thickness by inhibiting the secretory ability of the shell-secreting glands of the uterus. Berg, Bearse, and Hamilton (1947) observed that Newcastle disease caused some birds in their flock to lay thin-shelled eggs. In selecting future breeding stock, especially when this is done on a family basis, poultry breeders should keep these points in mind.

Breeding for Better Shell Quality. The fact that some of the egg-shell characters previously discussed, as well as certain others, have a hereditary basis has been demonstrated by several investigators. Results secured by Willard and Shaw (1909), Taylor and Martin (1928), Romanoff (1929), Almquist and Holst (1931), Halnan (1935), and Baskett, Dryden, and Hale (1937) indicated the heritability of such characters as shell percentage of total egg weight, shell porosity, thickness, and breaking strength. Hutt (1949) submitted data from various investigators with respect to the superiority of White Leghorn eggs over the eggs of several general purpose varieties in different egg characters.

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to improve shell quality is to determine the relative loss in weight of eggs when incubated for 14 days at 99 5° F at 60 per cent relative humidity, as was done by Quinn, Gordon, and Godfrey (1945)

From an original flock of White Leghorns, two lines were developed differing in egg-weight loss   Cockerels for breeding purposes were selected from families of full-sisters whose eggs showed the least and the greatest loss in weight, respectively   The females used for breeding

FIG 95 Showing the difference in percentage loss in weight of eggs during 14 days of incubation at 99 5° F , between two strains of White Leghorns developed by selection and breeding from the same original flock   After 7 years the difference in weight loss between the two lines of breeders was 5 3 per cent and between the two lines of progenies 3 6 per cent (Quinn Gordon and Godfrey 1945)

purposes consisted of (1) progeny-tested dams and (2) pullets from families of full-sisters whose eggs showed the least and the greatest loss in weight, respectively   The eggs of all the progeny of each line were tested for loss in weight   The line showing the least loss in egg weight laid eggs with better shells than the line showing the greatest loss in egg weight   The extent to which the lines differed during 7 years of selection and breeding is shown in Fig 95

It is clearly apparent from Fig 95 that shell quality, as determined by loss in egg weight during incubation, is inherited and can be improved by progeny-testing dams and by selecting cockerels and pullets for breeding purposes from families in which the full-sisters' egg-weight loss is the least   In eggs having good shell quality, the thick white does not break down so readily in warm weather as in eggs having poor shell quality

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Knox and Godfrey (1938) showed that the percentage thick albumen of total albumen decreased from October through June of the first laying year, indicating a seasonal influence on this character Much the same situation was found true for eggs laid by yearling and older hens Jeffrey (1941b) compared the seasonal rate of decrease in thick albumen between April-hatched and November-hatched pullets and

Fig 96 In grade AA the thick white stands up well around the yolk whereas in grades A and B there is a progressive breakdown of the thick white and in grade C the thick white has almost completely disappeared (Van Wagenen and Hall 1936)

observed that during the summer months the April-hatched pullets' eggs had relatively less thick white than the November-hatched pullets' eggs

The fact that the percentage thick albumen of total albumen is a characteristic dependent on the individual hen was apparently first demonstrated by Holst and Almquist (1931) and later confirmed by Munro (1938) The fact that the percentage thick albumen of total albumen is inherited was demonstrated by Lorenz, Taylor, and Almquist (1934) and Knox and Godfrey (1938) Working with White Leghorns and Rhode Island Reds, Knox and Godfrey (1934) found that White Leghorn eggs had a significantly greater percentage of thick albumen than did Rhode Island Red eggs Van Wagenen and Hall (1936) submitted evidence indicating that the percentage thin albumen of total albumen is inherited

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Figure 98 shows that the original flock from which the two lines were developed laid eggs whose thick albumen was approximately 50 per cent of the total albumen. After 5 years of selection the percentage of thick

Fig 99 Left after 2 weeks in incubator this heat-resistant thick white has shrunk only 15 per cent. Right 65 per cent of this non heat resistant thick white has disappeared after 14 days of incubation. Contrast with heat resistant white at the left (Quinn 1948)

albumen in the high-line progeny was 64 0 and in the low-line 46 5. Judging by these results, it should be possible for poultry breeders to improve their strain of birds with respect to the relative percentage of thick albumen by adopting a sound progeny-testing program

Quinn (1948) and Quinn and McNally (1950) reported that it is possible to breed for resistance of thick white to deterioration from excessive heat. After 7 years of progeny-testing White Leghorns, hens were produced that laid eggs whose thick albumen resisted deterioration when subjected to 100° F for 14 days (see Fig 99)

Yolk Quality. It is well known that in some cases the kind of diet fed the laying flock affects the color of the yolk. For instance, diets containing an abundance of green feed yield eggs with deep yellow yolks whereas diets lacking carotinoid pigments yield eggs with very pale

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Blood clots and spots are due apparently to hemorrhages that occur between the inner lining of the follicle and the vitelline membrane of the yolk some time before ovulation, or at the time of ovulation, or

Fig. 100. Types of blood clots and spots in eggs A, blood streak, B, two blood clots not attached to the yolk, C, blood sheet, D, combination of blood clot, blood sheet, and blood streak, E, blood streak, F, red blood clot, G, brown blood clot, H, pinkish tan "meat" spot, I, "meat spot" with dark center and white rim, J, blood clot and blood streak (Nalbandov and Card, 1944)

much less frequently in the magnum section of the oviduct (Burmester and Card, 1938) In this discussion, the only distinction made between blood clots and spots is with respect to size. Blood clots and spots, especially clots, may vary in color from white to bright red to dark brown, depending upon the extent to which the degeneration of the blood has taken place before the egg is opened Clots of degenerated blood have sometimes been referred to as "meat spots" This is a misnomer because the clots consist of red blood corpuscles, for the most part, enclosed in a protein layer. Sharma (1950) pointed out that white "meat spots" are formed in the oviduct by the coagulation of albumen surrounding a degenerated blood clot.

Effect of Environmental Factors. Card and Nalbandov (1944) reported that birds given access to grass range produced eggs with fewer blood

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by birds which survived the first laying year tended to be higher than in eggs laid by birds which died during the laying year

Age of Layers Concerning the incidence of blood spots in eggs in relation to the age of layers, Nalbandov and Card (1944) reported that the incidence was considerably greater during the first laying year than during the second laying year and somewhat greater during the second than the third laying year On the other hand, Sharma (1949) reported that the incidence of blood spots was highest in the second laying year

Shell Color Upon the basis of the examination of the broken-out appearance of Rhode Island Red eggs that were classified as having light brown shells and dark brown shells, respectively, Jeffrey and Walker (1950) reported that 34 8 per cent of the light brown eggs had blood clots and spots whereas 49 4 per cent of the dark brown eggs had blood clots and spots (the designations of "colored meat spots" and "white meat spots" used by Jeffrey and Walker were considered to be degenerated blood clots) Whether certain birds laid the light-brown-shelled eggs and certain other birds laid the dark-brown-shelled eggs was not reported Also, the incidence of blood clots and spots in light-brown-shelled eggs as compared with their incidence in dark-brown-shelled eggs laid by the same bird was not reported The F_2 progeny secured from reciprocal crosses between White Leghorns and Rhode Island Reds were classified into three groups (1) those laying white-shelled eggs, (2) those laying tinted eggs, (3) those laying light-brown-shelled eggs The percentage of blood clots and spots in the eggs of these three groups of F_2 birds was as follows 34 2, 22 5, and 42 0 respectively

Breed and Variety Differences With respect to differences in the incidence of blood clots and blood spots according to breeds, the observations of several investigators vary somewhat Hall (1939) reported the following percentages of eggs with blood spots White Wyandottes, 1 0, Barred Plymouth Rocks, 6 0, Rhode Island Reds, 7 8, White Leghorns, 5 7 Quinn and Godfrey (1940) observed that the percentage of blood spots was very much less in White Leghorns than in White Wyandottes, whose blood-spot percentage in eggs was about half that in Rhode Island Red eggs Nalbandov and Card (1947) reported considerably higher percentages of blood clots in the eggs of general-purpose breeds than in White Leghorn eggs Jeffrey and Walker (1950) found little difference among White Leghorns, Barred Plymouth Rocks White Plymouth Rocks, and Rhode Island Reds with respect to the percentage of blood spots, but they noted that the general-purpose birds far exceeded the White Leghorns with respect to the percentage of blood clots

by birds which survived the first laying year tended to be higher than in eggs laid by birds which died during the laying year

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Eggs with Two or Three Yolks. Most of the double-yolked eggs result from two ova that develop in the ovary at the same rate, mature at the same time, and as a consequence are ovulated simultaneously A few double-yolked eggs apparently result from the ovulation prematurely, by one day, of an ovum so that it "catches up" with the ovum that was ovulated in natural sequence the previous day Other double-yolked eggs are said to result when the mouth of the oviduct receives an ovulated ovum directly from the ovary either immediately before or after the engulfing of an ovulated ovum that had dropped into the body cavity For further details, see Curtis (1914b, 1915) and Conrad and Warren (1940) Triple-yolked eggs originate in the same way as double-yolked eggs

Eggs within Eggs. In some cases, the enclosing egg contains no yolk but the enclosed egg is complete in all parts In other cases, the enclosing and enclosed egg each contain a yolk and are otherwise complete Asmundson (1933a), who reviewed several earlier reports of different kinds of eggs within eggs also mentioned the case of a double egg comprising a small, yolkless dwarf egg enclosed in a normal egg According to Asmundson, these different kinds of eggs within eggs are formed when the enclosed egg returns from the uterus to the upper part of the oviduct, where it is joined by a yolk with surrounding albumen or with albumen only The completed egg and additional material are then enclosed in shell membranes and then pass to the uterus, where shell encloses the whole mass A double egg, the enclosed and the enclosing egg each having a yolk, was described by Romanoff and Hutt (1945) and was reported to be formed in the same way as that described by Asmundson A slightly different type of double-yolked egg was described by Hutt (1946), the second yolk being still enclosed in its follicle, the stalk of which protruded through the large end of the shell Immediately surrounding the protruding stalk, there was only a very thin covering of shell Apparently, the mouth of the oviduct had engulfed the first ovum (which had ovulated normally) and then had grasped the second ovum, still contained in its follicle

Other Abnormalities Another case in which the mouth of the oviduct engulfed a follicle with its contained yolk was reported by Hutt (1939) This follicle must have passed through the entire oviduct rather rapidly, since only a small amount of albumen had been secreted in the equatorial region of the follicular layer surrounding the yolk

Parker and Kempster (1940) described a normal but thin-shelled egg from the large end of which protruded a brownish mass of material connected with a portion of the ovary which contained about 25 ova in

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12 · Selection Methods

The ultimate goal of any breeding program is to have a high proportion of desirable individuals in the population. The desired type will usually involve not one but several economic characters. Since no one animal ever combines all the best characters, we must be reconciled from the beginning to compromise in the selection of future breeding stock. With respect to the perpetuation of the race, each individual constitutes a new and temporary combination of genes which are taken as samples from the genes of the parents. It is in this sampling process that the breeder is able to exercise some degree of control, thus changing the new population so that it is a little different from the preceding one. It is not possible to control which gene of any given pair goes to the new individual, however, it is sometimes possible to select parents so that it will make no difference which gene of the pair happens to be used, for example, parents that are homozygous for the gene in question.

There are few if any characters of economic importance in poultry that are determined by a single pair of genes or even by a few pairs of genes. The inheritance of the recessive white color approaches this condition, the birds are either colored or not colored, with practically no intermediate condition. A character so inherited exhibits so-called discontinuous variability. Most of the characters of importance in poultry, however, show a continuous type of variation, indicating that many genes are concerned in determining the character. An example of this type of inheritance is found in the study of body weights (Jull and Quinn, 1931). When small birds are mated to large ones, the F_2 progeny shows a wide degree of variation. Some are nearly as large as the large parent, and some are nearly as small as the small parent, with most individuals ranging somewhere between the two parents. When the data representing the measurements for such a character are plotted on a frequency curve, a normal bell-shaped distribution results. The greater the number of genes involved in determining the character, the smoother will be the frequency curve (Lush 1945). A frequency distribution of the weights of 10-week-old New Hampshire broilers grown

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FIG. 101 Frequency distribution showing the number of individuals per weight group. The data include the 10-week weights of 800 male and 800 female New Hampshire chickens grown under commercial production conditions

Fig. 101 Frequency distribution showing the number of individuals per weight group The data include the 10-week weights of 800 male and 800 female New Hampshire chickens grown under commercial production conditions

in which the desirable genes predominate. A third factor affecting rate of change is the accuracy with which individuals with a desirable genotype can be identified. This relationship between genotype and phenotype is another phase of breeding and will be discussed below as heritability.

Heritability. The phenotypic expression of all characters is influenced by both environment and heredity, and it is useful to know the relative importance of each. It is helpful to know something about the heritability of a character in determining whether the record of an individual can be wisely used in estimating its breeding worth. If a bird is white, color being highly heritable, we can be sure the individual has the genotype for white color. However, if a hen lays 200 eggs, egg production having a low degree of heritability, it may have a genotype that usually results in 175 eggs under unfavorable environmental conditions or one that usually results in 235 eggs under the most favorable environmental conditions. Heritability, as defined by Lush (1949), is "the fraction of the observed or phenotypic variance which was caused by differences between the genes or genotypes of the individual"

Heritability can be measured by several different means but, regardless of the mechanics used, the essential factor is to determine the relative importance of heredity and environment in contributing to the variation among individuals of a given population. It is easy to see that the difference between identical twins would be primarily due to environment, however, because of the limited number of identical twins available, experimentation can seldom be employed.

The closest approximation to the condition found in identical twins is highly inbred lines that are homozygous for most genes. The variation within such lines would be due primarily to environment. The variation within inbred lines can thus be compared with the variation within random breeding populations to secure an estimate of heritability. Another method of estimating heritability is to study the relationship between parent and offspring. This method is rather commonly used, but it has the disadvantage that the estimate is apt to be too high, since the parent and offspring are, in general, apt to have some environmental factors in common. This objection, however, is not serious in the poultry field.

Probably the most widely used method of estimating heritability is to study the sources of variation within a population. Heritability is studied by calculating differences among individuals rather than by using absolute values. In statistical procedures, these differences are used to secure a value which is a measure of variation and is called variance. The mathematics necessary for determining heritability

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are influenced by the stock used and by environmental conditions It is observed in Fig 102, however, that egg production and sexual maturity are relatively less heritable than are egg weight and body weight This knowledge enables us to use the appropriate method of selection to make the most rapid progress

If a character is highly heritable, then the individual's record should be given first consideration In this case, the phenotype is a reliable expression of the genotype If a character has a low degree of heritability, meaning that the phenotypic expression is not a very reliable estimate of the genotype, then it will be necessary to use the sib test, or progeny test, or some other method of making selection in which less importance is attached to the record of the individual and more importance to estimates of its genotype

A further use for heritability data is indicated by Lerner (1947), who suggested that, when the heritability of a character is known and the difference between the records of the flock as a whole and the records of the stock used for breeders are likewise known (called selection differential), it is possible to forecast the amount of improvement expected in each generation

Lerner stated that, if the selection differential between the egg production of the flock as a whole and that of the birds selected as breeders is 50 eggs and if degree of heritability is 10 per cent, then the production of the offspring of the selected group would be expected to be improved by 50×10 per cent, or 5 eggs per generation In practice, however, a complication arises in that egg production is not expressed by the males hence, the males must be selected on the basis of the record of their sisters or on the record of their progeny Lerner working with the egg-production records of the University of California flock, found that the greater the number of sisters or progeny that are tested, up to certain limits, the greater the increase of heritability

This point is well illustrated by the data in Table 29, which shows the heritabilities for various bases of selection The decrease in selection

TABLE 29

A SUMMARY OF THE SELECTION DIFFERENTIALS AND HERITABILITIES FOR THE SELECTION BASES USED BY LERNER (1947)

Statistics	*Selection Basis*	*Sires*	*Dam*
Selection differential (eggs)	Individual record	None	99 1
	Record of sisters	26 0	39 8
	Record of progeny	24 4	29 0
Heritability (per cent)	Individual record	None	4 5
	Record of sisters	15 5	13 8
	Record of progeny	45 2	15 5

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Fig 102 An essay of estimates of heritability from various sources Each estimate is intended for the respective investigators 1 and Hazel and Lamoreux, 1917, C, Lerner, 1915, D, Lerner, Asmundson, and Cruden, 1948, G, Munro, 1936, H, Munro, Bird, and Hopkins, 1937, I, Shoffner, 1948, J, Waters, 1941 (2) Data from the following sources added by author K, El-Ibiary and Shoffner, 1950, L, Robertson and Lerner, 1949, M, Lush, Lamoreux, and Hazel, 1918 N, Lerner and Cruden 1951

Heritability, per cent

Heritability, per cent	Egg production	Sexual maturity	Egg weight	Body weight	Keel length	Shank length	Body depth	Thyroid weight	Hatchability	Viability
37		37A								
35	35A 34I									
33		33C 32A								
32				32B	32K					
31	31H									
30					30K					
27	27B									
26	26A 26S									
25	25G 25A 25A 25N									
24	24A 24A						24K			
23	23E									
22		22E			22K					
20	20G									
17		17A								
16	16A	16C				16K			16I	
14						14K	14K	14K		14M
13										13E
12		12A								
9						9K	9K			9L
8								8K		8M
3						3K				

Fig. 102 An array of estimates of heritability from various sources. Each estimate is initialed for the respective investigators. 1 and 2 (1) Data from the following authors were compiled by Shoffner and Sloan, 1948 A, Comstock, Bostian, and Dearstyne, 1947 and Hazel and Lamoreux, 1917, C, Lerner, 1945, D, Lerner, Asmundson, and Cruden, 1947 E Lerner and Taylor 1943, F, Lush, Lamoreux, and Hazel, 1948, G, Munro, 1936, H, Munro, Bird, and Hopkins, 1937, I, Shoffner, 1948, J, Waters, 1941 (2) Data from the following added by author K, El-Ibiary and Shoffner, 1950, L, Robertson and Lerner, 1949, M, Lush, Lamoreux, and Hazel, 1948 N, Lerner and Cruden 1951

greatest degree of inbreeding in animals is secured by full-brother-full-sister matings

Essentially, the coefficient of inbreeding is determined by the number of individuals appearing in both the maternal and paternal ancestry It is found by calculating the probability that an offspring will receive the same allele of any given pair from both the sire and the dam When this occurs, the individual becomes homozygous for that gene pair, hence, we see that the coefficient of inbreeding gives us some idea of the degree of homozygosity It must be remembered, though, that the coefficient of inbreeding does not tell us what percentage of the total number of genes are homozygous but rather what percentage of the genes that were heterozygous at the beginning of the inbreeding have become homozygous For example, say that there are 5000 gene pairs in the White Leghorn, 1000 of which are in the heterozygous state with a gene frequency of 0 5 If full-brother-full-sister matings are practiced for one generation, 25 per cent inbreeding will result (see Fig 103) This will mean that on the average 25 per cent of the 1000 gene pairs which were heterozygous are now homozygous In other words, there would be 4250 homozygous pairs and 750 heterozygous pairs of genes

If the gene frequency for a given gene is 0 5, then the probabilities of its becoming homozygous dominant and homozygous recessive are equal It is unlikely, however, that the gene frequency for a very large proportion of the genes in any family will be 0 5 If the frequency for the dominant form of the allele is 0 8 in a particular family, then upon inbreeding there is greater probability that the gene will become homozygous dominant than homozygous recessive If in another family the frequency for the dominant allele is only 0 3, then upon the inbreeding of this family the gene probably will become fixed or homozygous in the recessive state It must be borne in mind, however, that we are here considering only probabilities and that it is entirely possible for the reverse to happen

As mentioned earlier, the degree of inbreeding indicates the probability of an offspring's receiving a like allele of any pair from both sire and dam Inbreeding involves matings made in such a way that dam and sire are related or have a common ancestor Combining these facts leads us then to determining how many gene segregations (or generations) have taken place between offspring and the ancestors which are common to both dam and sire This may be demonstrated by studying the following diagrams showing two generations of half-brother-half-sister matings The pedigree of individual *J* is presented at the left in the conventional manner and at the right schematically to facilitate the tracing of genetic pathways

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value for F_a is too low to be of much consequence In the event that there has been some previous inbreeding in the stock, the value for F_a in the formula becomes important. Let us assume that in the above example the individual B is inbred to the extent of 25 per cent This would change the above calculation to the extent that the value for the pathway $H–L–B–F–I$ would be multiplied by $1 + 0\ 25$, as follows

$$H–L–B–F–I = 4 + 1 = (\tfrac{1}{2})^5 = 3\ 125 \times 1\ 25 = 3\ 906$$

Thus the value for this pathway is increased from 3 125 per cent to 3 906 per cent because of the fact that the common ancestor B was inbred to the extent of 25 per cent

While it is not expected that most practical breeders will spend the time to calculate the inbreeding of each bird, they should be familiar with the genetic principles involved and the rate at which the inbreeding coefficient will increase with their system of breeding Wright (1931) estimated that, when a population is kept closed to outside breeding stock, the amount of the remaining heterozygosity lost per generation will be $1/8M + 1/8L$, where M and L are the numbers of males and females, respectively, reaching breeding age in each generation In a poultry flock, the fraction $1/8L$ would be very small because of the large number of females, hence, it can generally be disregarded Only the $1/8M$ portion of the formula is then left to be considered When a breeder has as few as eight single-male matings, the loss of heterozygosity would then become $1/(8 \times 8)$, or about 1 5 per cent per generation This amount of inbreeding would not be expected to cause any trouble

The above observation along with an examination of Fig 103 indicates that most systems of mating now in practice do not lead to much inbreeding

When intensive inbreeding is practiced (such as successive generations of full-brother-full-sister matings used to produce inbred lines for hybridizing), low viability usually results In these highly inbred lines, there are reduced hatchability and egg production, retarded growth, and increased mortality Also, many physical defects, lethals, and monstrosities appear Schnetzler (1948) estimated that these physical defects and mortality during the first 8 weeks eliminated 30 to 50 per cent of the stock during the first 3 years of full-brother-full-sister matings The effects of inbreeding are more noticeable in some strains than in others, and there is no way of knowing which strains will best withstand close inbreeding

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$$H-C-B-F-I = 4 + 1 = (\frac{1}{2})^5 = 3.125 \times 1.25 = 3.906$$

Thus the value for this pathway is increased from 3.125 per cent to 3.906 per cent because of the fact that the common ancestor B was inbred to the extent of 25 per cent.

While it is not expected that most practical breeders will spend the time to calculate the inbreeding of each bird, they should be familiar with the genetic principles involved and the rate at which the inbreeding coefficient will increase with their system of breeding. Wright (1931) estimated that, when a population is kept closed to outside breeding stock, the amount of the remaining heterozygosity lost per generation will be $1/8M + 1/8L$, where M and L are the numbers of males and females, respectively, reaching breeding age in each generation. In a poultry flock, the fraction $1/8L$ would be very small because of the large number of females, hence, it can generally be disregarded. Only the $1/8M$ portion of the formula is then left to be considered. When a breeder has as few as eight single-male matings, the loss of heterozygosity would then become $1/(8 \times 8)$, or about 1.5 per cent per generation. This amount of inbreeding would not be expected to cause any trouble.

The above observation along with an examination of Fig. 103 indicates that most systems of mating now in practice do not lead to much inbreeding.

When intensive inbreeding is practiced (such as successive generations of full-brother-full-sister matings used to produce inbred lines for hybridizing), low viability usually results. In these highly inbred lines, there are reduced hatchability and egg production, retarded growth, and increased mortality. Also, many physical defects, lethals, and monstrosities appear. Schnetzler (1948) estimated that these physical defects and mortality during the first 8 weeks eliminated 30 to 50 per cent of the stock during the first 3 years of full-brother full-sister matings. The effects of inbreeding are more noticeable in some strains than in others, and there is no way of knowing which strains will best withstand close inbreeding.

a third inbred line is referred to as a three-way cross. A four-way cross is made by mating the offspring from two different single crosses (see Fig 104). The egg production of the inbred females is apt to be too low to make the use of a single cross practical commercially, hence, it is necessary to use either a three-way or four-way cross. In this procedure, the females are themselves hybrids and have better egg production than their inbred dams. Most of the hybrids so far developed have been the result of crossing inbred lines from different breeds, since inbred lines originating within a strain or breed may be too closely related to give the maximum benefit. Factors such as egg color, broodiness, plumage, and physical characteristics must be considered when making the crosses between different varieties or breeds. The expression of these characters, as well as those of egg production, egg size, etc, are influenced by the manner in which the inbred lines are put together, that is, whether the male or female from the respective inbred lines is used and, in three- and four-way crosses, which inbred lines are used with other inbred lines.

It thus becomes evident that, in order to utilize hybrid vigor, the poultry breeder not only must develop good inbred lines that are relatively viable but also, and this is equally important, must wisely determine which of these lines to use and in what manner. These considerations emphasize the fact that the development of hybrid poultry entails a good deal of time, labor, and expense and should be undertaken only by those breeders who have sufficient capital and facilities to develop and test enough lines to have some assurance of success.

Reciprocal Recurrent Selection. A new kind of breeding and selection system has been proposed that appears to offer considerable promise. The new system, known as reciprocal recurrent selection or simply as reciprocal selection, may prove to yield the maximum benefits of hybrid vigor without requiring the expensive and laborious task of developing inbred lines.

It has long been known that, when certain noninbred individuals are mated, the progeny produced is superior to that produced by other, similar matings even though all parents involved are from families of equal breeding worth. This phenomenon is known as "nicking." Recurrent selection attempts to develop strains which, when crossed, yield progeny superior to either parental strain. Selection is based not on the performance of the individuals within the strain but upon their ability to combine well with other strains or breeds. The objective of such selection is to sort out and fix those genes within each strain or breed that combine well or "nick" to produce the maximum of hybrid vigor. In order that the strains or breeds remain more or less flexible for

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Selection Guides. The ultimate success of any breeding program is largely dependent upon the wisdom with which the prospective parents are chosen During the development of most of our standard breeds, breeders based their selection primarily on the merit of the individual Without belittling the contributions of the past, it must now be pointed out that for the further improvement of most characters, individual

		Relative Merit of Progeny										Average of Dam s Progeny	Average of Sire s Progeny
Sire	Dam	1	2	3	4	5	6	7	8	9	10		
X	A		x				xx	x	xx	xx	xx	7 5	
	B			x		xx	xxx	x	x	x	x	6 5	5 8
	C	xx	xxx	x	xx	x				x		3 3	
Y	D				x	xx	xxx	x	xx	x		6 4	
	E						x	x	xx	xx	xxxx	8 7	7 5
	F				x	x		xxx	xxx	x	x	7 3	
Z	G		xx	xxx	xx	x	x				x	4 2	
	H			x	xx		xxx	xx	x	x		6 0	4 9
	I		x	xx	xxx	xx	x		x			4 4	

Fig 106 Hypothetical distribution of individuals within families according to t eir relative merit

selection must be supplemented with family selection or progeny testing

Figure 106 is presented to illustrate the mechanics of family selection and the information that can be gained from such records This figure represents the mating of three males, *X*, *Y*, and *Z*, to three females each (*A–I*), all of which we assume had similar individual records The individual merit of the daughters thus produced is represented by the values from 1 to 10, the latter being the most desirable For the sake of discussion, assume that these values are for the one particular character being considered In calculating a dam's family average, the merit of all her daughters is averaged in the following manner Dam *A*, for example, produced 1 daughter with a relative value of 2, 2 daughters

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	A		x				xx	x	xx	xx	xx	7 5	
X	B			x		xx	xxx	x	x	x	x	6 5	5 8
	C	xx	xxx	x	xx	x				x		3 3	
	D				x	xx	xxx	x	xx	x		6 4	
Y	E						x	x	xx	xx	xxxx	8 7	7 5
	F			x	x			xxx	xxx	x	x	7 3	
	G		xx	xxx	xx	x	x				x	4 2	
Z	H			x	xx		xxx	xx	x	x		6 0	4 9
	I		x	xx	xxx	xx	x		x			4 4	

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daughter   If we assume again that 20 per cent of the daughters would be selected for breeding to increase egg production, one might save all the daughters of dams *A*, *E*, and *F* that had a score of 8 or better   In making use of family records, the question always presents itself what to do about the superior individuals in the poor or mediocre families and the inferior individuals in the superior families   In breeding for egg production, neither of these categories should be selected for breeding purposes   The relative futility of selecting for egg production on the basis of individual records alone was pointed out in Chapter 10

The value of family records is even more fully appreciated in the selection of the male   Since one male is mated to fifteen or more females he contributes fifteen or more times as much genetically to the next generation as any one female, and his selection should receive considerable attention   In selecting one male from the progeny represented in Fig 106, first choice would be the most outstanding individual phenotypically among the sons of dam *E* and sire *Y*, since the daughters of dam *E* had a higher average score than the daughters of all other dams and the daughters of sire *Y* had a higher average score than the daughters of the other sires   This would not be positive assurance, of course that the male thus selected would produce superior progeny, but the probabilities would be much better than they would be if we knew nothing of his full sisters' and half-sisters' performance   The above discussion is meant to imply not that there is no longer a place for individual selection but rather that one must supplement the other   According to Lush (1947), the most efficient kind of a continuous breeding program is one in which emphasis shifts from individual selection to family selection as more attention is given to characters that are less and less heritable

Progeny Testing.   The most accurate estimate of an animal's breeding worth is an evaluation of its progeny when it is mated with several different mates   Reference to Fig 106 reveals that dams *A* and *E* produced daughters that on the average were superior to those of the other dams shown   This is the best proof that these dams have the desirable genotype and they and their progeny should be used in future breeding operations   Among the sires represented in Fig 106 sire *Y* produced progeny superior to either of the other two sires In this example, however, the males have not been mated to a sufficient number of females to establish fully the breeding worth of the different sires

In normal breeding operations, each male would be mated to eight or more females representing several full sister families   The performance of each male's progeny under such a system is highly representative of his breeding worth

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If the strain is relatively weak in any one of these characters, it will be necessary to put more emphasis on that character. As the breeding program progresses, the value assigned to each character can be altered or a change can be made in the number of characters considered. Whether an individual would be culled or used for breeding would thus depend on its total score in relation to the score of all other progeny-tested birds. It is thus that we return to the original premise of this chapter, that successful breeding involves a succession of compromises. No single bird is apt to be superior in all characters, and it is the poultry breeder's role to bring together as many of the desirable characters as possible in the progeny produced.

PROBLEMS

1. What would be the expected gene frequency for gene I in the progeny of a mating of a heterozygous male (Ii) × homozygous females (II)?

2. Within a flock, would you expect the degree of heritability of a given character to decrease or increase when the stock is inbred? Why?

3. How is it possible for the dam to influence the weight of her progeny at 4 weeks of age other than by her contribution of genes influencing rate of growth? What is the term for this phenomenon?

4. What is the fundamental difference between the breeding program to develop hybrid pullets (the progeny of crossed inbred lines) and the breeding program based on reciprocal recurrent selection?

5. What method of selection would be most advantageous to employ for increasing egg size?

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